Early Life History and Fisheries Oceanography
New Questions in a Changing World

By Joel K. Llopiz, Robert K. Cowen, Martha J. Hauff, Rubao Ji,

Philip L. Munday, Barbara A. Muhling, Myron A. Peck, David E. Richardson,

Susan Sogard, and Su Sponaugle

CAPTION. Larval stage of selected fish (from left to right): armored searobin, largetooth flounder, bythitid brotula, and little tunny. *Photos by Cedric Guigand*

ABSTRACT. In the past 100 years since the birth of fisheries oceanography, research on the early life history of fishes, particularly the larval stage, has been extensive, and much progress has been made in identifying the mechanisms by which factors such as feeding success, predation, or dispersal can influence larval survival. However, in recent years, the study of fish early life history has undergone a major and, arguably, necessary shift, resulting in a growing body of research aimed at understanding the consequences of climate change and other anthropogenically induced stressors. Here, we review these efforts, focusing on the ways in which fish early life stages are directly and indirectly affected by increasing temperature; increasing CO_2 concentrations, and ocean acidification; spatial, temporal, and magnitude changes in secondary production and spawning; and the synergistic effects of fishing and climate change. We highlight how these and other factors affect not only larval survivorship, but also the dispersal of planktonic eggs and larvae, and thus the connectivity and replenishment of fish subpopulations. While much of this work is in its infancy and many consequences are speculative or entirely unknown, new modeling approaches are proving to be insightful by predicting how early life stage survival may change in the future and how such changes will impact economically and ecologically important fish populations.

BACKGROUND

Understanding the early life stages of fishes, and the processes influencing their survival, is at the heart of fisheries oceanography, along with the field's historical roots. In the early twentieth century, the founding father of fisheries oceanography, Johan Hjort of Norway, led international efforts to understand why important fish stocks yield such remarkably large variations in catch. While most researchers were focused on the movement of adults in and out of fishing grounds as a cause of recruitment fluctuations (Sinclair, 1997), Norway's enormous 1904 year class of herring inspired Hjort to think instead about the recruitment process—that is, the survival of the early life stages. This year, we celebrate the centennial of the publication of Hjort's (1914) seminal work entitled "Fluctuations in the great fisheries of northern Europe, viewed in the light of biological research" (see Browman, 2014). This is where Hjort first laid out his most enduring contribution to the field of fisheries oceanography, the critical period hypothesis, which posited that recruitment levels could be greatly influenced by the degree to which sufficient types and abundances of planktonic prey were available to millimeter-scale fish larvae as they first transitioned to exogenous feeding. In addition to the critical period hypothesis, Hjort also put forth his aberrant drift hypothesis (1914, 1926), a groundbreaking theory that highlighted the importance of variability in the transport and dispersal of eggs and larvae by ocean currents in shaping recruitment patterns. Thus, Hjort touched upon two of the three major challenges faced by fish larvae in the plankton: finding food and reaching suitable juvenile habitat. Real progress in understanding the third critical hurdle—avoiding predators—did not come for another 75 years (Bailey and Houde, 1989).

With Hjort laying the foundation for early life history research in the twentieth century, the race to solve the "recruitment problem" picked up considerable steam in the last quarter of the century (Houde, 2008), especially after David Cushing extended Hjort's critical period hypothesis to the entire larval period with his match-mismatch hypothesis (Cushing, 1974, 1990). This hypothesis emphasized the degree to which fish larvae and their planktonic prey overlap temporally (as determined by the timing of productivity blooms and fish spawning) as a key factor in determining larval survival and recruitment. The match-mismatch hypothesis has had a remarkable impact on the direction of larval fish research, and it laid the cornerstones for modern fisheries oceanography. A wave of early life history research led to the development of several other hypotheses on the mechanisms governing early life survival (Houde, 2008; Hare, 2014), yielded important discoveries in fish biology (e.g., daily increments in fish otoliths, or "ear stones"), drove advances in technology and techniques (e.g., coupled biological-physical models), and underpinned large-scale interdisciplinary programs (e.g., California Cooperative Oceanic Fisheries Investigations [CalCOFI], Fisheries Oceanography Coordinated Investigations [FOCI], Global Ocean Ecosystem Dynamics [GLOBEC]) that all contributed greatly to our ability to ask and answer interesting questions about survivorship in the early life stages of fishes. Some of the most important findings have elucidated the ways in which larval growth rates interact with overall mortality rates (growth-mortality hypothesis), largely due to reduced susceptibility to predation for a larva growing more quickly through its vulnerable planktonic period (Cushing, 1975; Houde, 1987, 1997; Anderson, 1988).

Building upon thorough reviews of the history and hypotheses of early life history and fisheries oceanography (Houde, 2008; Peck et al., 2012; Hare, 2014), we focus here on a pressing contemporary question in early life history research: the implications of global change and other anthropogenic impacts on fish early life survival. As in Hjort's time, planktonic fish larvae today still have to find food,

avoid predation, and end up in suitable juvenile habitat, yet a whole new suite of issues has emerged (Figure 1), and we must now consider how anthropogenically induced stressors affect natural processes. Specifically, how will climate-driven warming and ocean acidification directly and indirectly affect the life histories of planktonic larvae in their journey from spawning sites to juvenile nursery areas? How will ocean productivity change in magnitude as well as in time and space, and how will dynamics of productivity, zooplankton composition and abundance, and spawning output (in light of fishing pressure) influence early life survival and recruitment? How will ocean currents be impacted by climate change to affect larval transport and

population connectivity? Perhaps most importantly, how will all of these ongoing and impending global changes interact to affect the early life stages of fishes? Our goal here is to review some of the progress made in addressing these important questions, and to call attention to critical knowledge gaps yet to be filled.

TEMPERATURE EFFECTS

The increase in ocean temperatures throughout the next century will have major implications for the structure and functioning of marine ecosystems. With average sea surface temperatures potentially rising 3°C or more by the year 2100 (Collins et al., 2013), effects on fish early life stages inhabiting those surface waters could be profound. Rates and magnitudes

of change will likely vary regionally; temperatures near the equator, for example, should increase more rapidly than those at higher latitudes (Collins et al., 2013; Kirtman et al., 2013). Tropical larvae therefore may be subject to more dramatic temperature shifts, and they may also be particularly sensitive to increases, given that they are adapted to relatively narrow and stable thermal regimes (Tewksbury et al., 2008). Polar populations, too, are generally stenothermal, and they might be similarly sensitive to warming. Because mid-latitude fish populations are already subject to a wider range of temperatures, partly due to interdecadal fluctuations in circulation and surface heating in those regions (Wang et al., 2010), they could be more tolerant of temperature variation than their tropical and polar counterparts. Nevertheless, fish early life stages across latitudes will be affected by changing temperatures, whether by acute or chronic (i.e., sublethal) mechanisms.

In both embryos (fertilized eggs and yolk-sac larvae) and exogenously feeding larvae, lethal temperatures exist at which survival is simply not possible. Surprisingly, protocols used to determine the critical limits that define the thermal niches of juvenile and adult fishes (Pörtner and Peck, 2010) have not been applied to embryos or larvae. Thus, it is difficult to compare whether eggs and larvae of a given species have narrower or wider thermal windows than later life stages (Rijnsdorp et al., 2009). However, across all life stages, tropical species exist near their thermal optima (Rummer et al., 2014) and upper
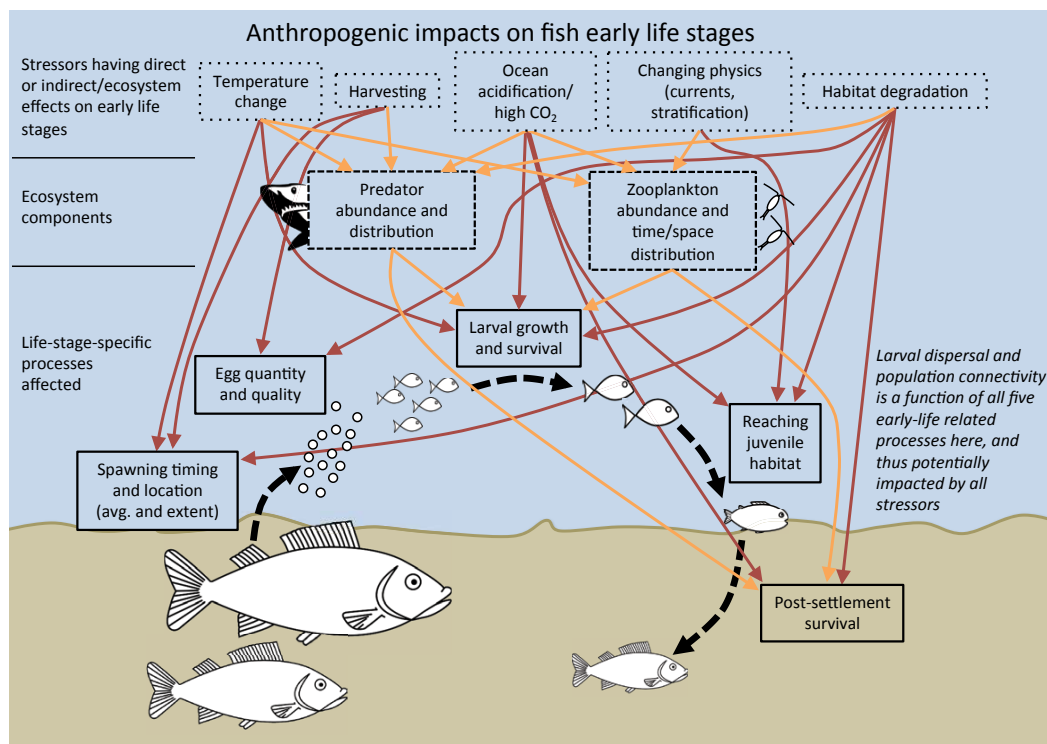

FIGURE 1. Schematic of the potential effects of climate-related and other anthropogenically induced changes on fish early life history. The complexity and potential for interactions of effects are evident from the many arrows from the potential stressors (dotted boxes) that are shared by each influential ecosystem component (i.e., predators and prey of early life stages denoted in dashed boxes) and early life stage process (five solid boxes). Dark red lines are direct effects on early life stages, while orange lines indicate effects on predators and prey of early stages that can, in turn, impact early life survival. Patterns of larval dispersal and population connectivity can vary with variability in all five early life stage processes depicted here, and thus be impacted by all anthropogenic stressors. It is worth noting that this diagram is not exhaustive in the number of potential effects or stressors, and that the stressors are broad (e.g., "habitat degradation" could range from chemical pollution to sound pollution, pelagic environments to benthic) and are not mutually exclusive (e.g., temperature changes are likely to cause changes in the physics of the ocean, and temperature can be the ultimate or proximate cause of habitat degradation). Further, to reduce complexity, interactions among early life stage process boxes (e.g., egg quality and larval growth and survival) are not included.

thermal limits, while temperate species tend to have the widest thermal windows (e.g., from 3° to 19°C in Atlantic herring).

Although some species may tolerate a range of temperatures, thermal variability has important effects on growth and survivorship of marine fish early life stages (Houde, 1989; Pepin, 1991). Because fish eggs and larvae are poikilothermic (cold-blooded), these effects are largely a function of the kinetics of cellular-level processes, but the directionality of change—whether key rates increase or decrease—can depend on each organism's particular thermal niche (Hutchinson, 1957). Both the hatch rate of embryos and the rate of embryo development (fueled by yolk utilization) increase with increasing temperature (Pepin, 1991; Peck et al., 2012). Cold-temperate species such as winter flounder take 30 days to hatch at 2°C but hatch after about one week at 12°C. By comparison, tropical species can hatch in less than one day at temperatures >25°C. The time it takes for newly hatched larvae to exhaust their endogenous yolk reserves ranges from about 400 hours to just 40 hours in species spawning at mean water temperatures of 5°C and 32°C, respectively (Peck et al., 2012), and within species, optimal temperatures exist where yolk utilization efficiency is highest, leading to larger sizes of larvae at hatch and/or at the time of yolk exhaustion.

After exogenous feeding has begun, temperature markedly affects all aspects of growth physiology and regulates the balance between energy gained from feeding and lost via metabolism. Metabolic rates of marine fish larvae have been measured since the 1960s, and the effect of temperature on oxygen consumption rate has been reported for several species. Q_{10} values (proportional increases in rates with a concomitant 10°C increase in temperature) typically range from ca.1.7 to 2.5, so at higher temperatures, substantially more food is required to fuel a given amount of growth (Houde, 1989). Theoretically, and given sufficient prey availability, rapid growth has the potential to improve larval fish survivorship. Faster growing larvae can more quickly outgrow gape (mouth-width)-limited predators, and tend to exhibit shorter pelagic larval durations (O'Connor et al., 2007), resulting in reduced exposure to the high risk of mortality during this particularly vulnerable life phase (Cushing, 1975; Houde, 1987; Anderson, 1988; Leggett and Deblois, 1994). Still, as temperature increases become more pronounced, any survival advantage conferred by faster growth at higher temperatures could be offset by a likely increase in instantaneous mortality rates. With increased prey consumption and activity (swimming) at higher temperatures come more frequent encounters with predators (Pepin, 1991). Changes in water viscosity with increasing temperatures could also undermine larval survival because of the relative Reynolds numbers of the larvae and their prey. Larval fish prey (e.g., copepod nauplii) are much smaller than the fish larvae themselves (often by an order of magnitude or more), and operate at much lower Reynolds numbers (meaning they experience much more viscous drag). As temperatures increase and viscosity is reduced, associated improvement in swimming performance or maneuverability should be proportionally greater for tiny prey than for larger fish larvae (Fuiman, 1986; von Herbing, 2002; Gemmell et al., 2013), so warmer temperatures could allow prey to be more adept at evading larval fish predators, thereby compromising larval fish feeding. Finally, if prey levels are limited for any reason—a very real possibility given the temporal and spatial shifts in prey availability likely to occur in the warmer ocean of the future (see phenology and productivity section)—mortality could stem from starvation due to thermally driven increases in metabolic costs in excess of available fuel (Pepin, 1991; Munday et al., 2009c).

Importantly, most studies investigating metabolic rates of larvae have examined "standard" or "routine" rates of respiration (RS and RR), while very few have examined the highest, active rates (RA) (Peck et al., 2012). Gaining a mechanistic, cause-and-effect understanding of how temperature influences growth potential in marine fish larvae (e.g., thermal reaction norms for growth) will require advances in methods that allow the full metabolic scope (RA-RS) to be estimated at different temperatures. For now, larviculture of commercially important species provides the best source of observations of temperatures optimal for growth because field growth data stemming from techniques such as otolith microstructure analysis are confounded by a lack of information on prey fields surrounding individuals.

OCEAN ACIDIFICATION AND HIGH CO$_2$

Rising CO_2 levels and ocean acidification present another threat to early life stages of marine fishes. The ocean absorbs approximately 30% of the carbon dioxide

Joel K. Llopiz (jllopiz@whoi.edu) is Assistant Scientist, Biology Department, Woods Hole Oceanographic Institution (WHOI), Woods Hole, MA, USA. **Robert K. Cowen** is Professor and Director, Hatfield Marine Science Center, Oregon State University, Newport, OR, USA. **Martha J. Hauff** is Guest Investigator, Biology Department, WHOI, Woods Hole, MA, USA. **Rubao Ji** is Associate Scientist, Biology Department, WHOI, Woods Hole, MA, USA. **Philip L. Munday** is Professor, ARC Centre of Excellence for Coral Reef Studies, and College of Marine and Environmental Sciences, James Cook University, Townsville, QLD, Australia. **Barbara A. Muhling** is Associate Scientist, Cooperative Institute for Marine and Atmospheric Studies, University of Miami, Miami, FL, USA. **Myron A. Peck** is Professor, Institute for Hydrobiology and Fisheries Science, University of Hamburg, Hamburg, Germany. **David E. Richardson** is Research Fishery Biologist, Northeast Fisheries Science Center, National Marine Fisheries Service (NMFS), National Oceanic and Atmospheric Administration (NOAA), Narragansett, RI, USA. **Susan Sogard** is Research Fishery Biologist, Southwest Fisheries Science Center, NMFS, NOAA, Santa Cruz, CA, USA. **Su Sponaugle** is Professor, Department of Integrative Biology, Oregon State University, Newport, OR, USA.

emitted from human activities such as fossil fuel burning, cement production, and land clearing (Sabine et al., 2004). The uptake of additional CO_2 leads to chemical changes that lower seawater pH and reduce the availability of carbonate ions (Doney et al., 2009; Feely et al., 2009). Average ocean pH is estimated to have declined by 0.1 units in the past 250 years due to the uptake of anthropogenic CO_2 and is projected to decline by a further 0.3 units by the end of this century if the current trajectory of CO_2 emissions is maintained (Feely et al., 2009; Collins et al., 2013). Furthermore, the atmosphere and the ocean surface are in approximate gas equilibrium; therefore, as CO_2 levels rise in the atmosphere, the pCO_2 of the ocean also increases (Doney et al., 2009).

Because marine fishes do not have extensive calcium carbonate skeletons, the rise in ocean pCO_2 is a greater concern than the decline in seawater pH and changes in the saturation state of carbonate ions. Higher ambient CO_2 levels (hypercapnia) can cause acidosis of the blood and tissues in fishes and other water-breathing organisms (Brauner and Baker, 2009; Heuer and Grosell, 2014). Juvenile and adult fishes generally have well-developed mechanisms for acid-base regulation and can cope with pCO_2 levels much higher than those projected due to climate change (Brauner and Baker, 2009; Esbaugh et al., 2012; Heuer and Grosell, 2014). However, in their early life stages, fishes are developing their physiological regulatory processes and at the same time undergoing rapid morphological change.

In general, eggs and embryos of marine fishes appear to be relatively tolerant to CO_2 levels within the range projected for the near future. Embryonic duration and hatching success are unaffected at high CO_2 in the majority of experiments conducted to date (e.g., Munday et al., 2009b; Franke and Clemmesen, 2011; Hurst et al., 2013). For larval fishes, however, there appears to be considerable variation in sensitivity to elevated CO_2, with some studies reporting

significant negative effects while others do not. For example, growth and survival declined at high CO_2 in larvae of two species, inland silverside (Baumann et al., 2012) and summer flounder (Chambers et al., 2014), but not in orange clownfish (Munday et al., 2009b), walleye pollock (Hurst et al., 2013), cobia (Bignami et al., 2013b), or European seabass (Pope et al., 2014). In fact, larval growth (size-at-age) increased in clownfish and seabass, and mortality also declined in seabass, when reared at elevated CO_2. Increases in morphological deformities and tissue damage have been observed in Atlantic cod (Frommel et al., 2012) and summer flounder (Chambers et al., 2014), but not in Baltic cod (Frommel et al., 2013) or other species. While much more research is needed, clearly there is high variability in the effects from and sensitivity of growth and mortality to high CO_2 among species, and thus the potential for significant differences in survival and recruitment.

One consistent effect observed in larval fishes reared at elevated CO_2 is increased otolith size (Checkley et al., 2009; Munday et al., 2011; Hurst et al., 2012; Bignami et al., 2013a; Maneja et al., 2013). While the implications of large otoliths are unknown, they could potentially include changes to hearing sensitivity or orientation (Bignami et al., 2013a), which could, in turn, affect navigation and the ability to reach juvenile habitat.

Unexpected effects of high CO_2 on larval and juvenile fishes are dramatic loss of sensory performance and altered behavior. Experiments over the past few years show that exposure of larval and juvenile fishes to elevated CO_2 affects olfactory (Munday et al., 2009a, 2014; Dixson et al., 2010) and auditory preferences (Simpson et al., 2011), visual reactivity (Chung et al., 2014), behavioral lateralization (Domenici et al., 2012), activity levels (Munday et al., 2010, 2013, 2014; Pimentel et al., 2014), and learning (Ferrari et al., 2012). The reason for this diverse suite of sensory and behavioral impairments appears to be interference of high CO_2 with the function of GABA-A

neurotransmitters (Nilsson et al., 2012; Chivers et al., 2014; Hamilton et al., 2014). These remarkable sensory and behavioral changes affect habitat selection and the timing of settlement to coral reef habitats (Devine et al., 2012), predator-prey interactions (Ferrari et al., 2011; Allan et al., 2013), and competitive abilities (McCormick et al., 2013). A major concern is that reduced responses to relevant sensory cues, altered activity levels, and impaired decision making could have serious implications for larval survival and recruitment to benthic juvenile populations (Munday et al., 2009a, 2010).

While some laboratory experiments have detected negative effects on larval growth and survival, conclusions about the impacts on fisheries must be made with caution. New studies show that transgenerational exposure to elevated CO_2 may help moderate impacts of acidification. In the first study of its kind, Miller et al. (2012) showed the negative effects of elevated CO_2 on the growth and survival of juvenile anemonefish were completely absent when their parents also experienced high CO_2. Similarly, in an elegant new field study, Murray et al. (2014) showed the effects of high CO_2 on survival of Atlantic silverside diminished when parents had also experienced higher CO_2 levels. While some behavioral effects of high CO_2 may also be partly restored by transgenerational exposure (Allan et al., 2014), other behavioral traits do not improve after long-term (Munday et al., 2014) or transgenerational exposure to high CO_2 (Welch et al., 2014). In this case, adaptation of sensory systems and behavioral responses through genetic selection would be required to overcome the negative effects of high CO_2. We have yet to determine whether such adaptation can occur fast enough to match the rapid pace of acidification and rising CO_2 levels, and future investigations into the effects of acidification on larvae will also have to consider the potential trade-offs and constraints of simultaneously adapting to ocean warming (Sunday et al., 2014).

Box 1. Larval Fish, Climate Change, and Habitat Models

As ocean temperatures have warmed in recent decades, a growing body of evidence has shown poleward shifts in the distributions of many fish species (Perry et al., 2005; Nye et al., 2009; Last et al., 2011). The result is often a shift in spawning grounds and in the times, locations, and environments in which fish eggs and larvae occur (Hsieh et al., 2009; Shoji et al., 2011). There is great interest in developing an ability to predict such shifts, both to validate past trends and to predict future climate change impacts. A group of techniques known as habitat models can help to achieve predictive ability.

Habitat models use environmental predictors to forecast the occurrence, abundance, or behavior of a species or community of interest (Guisan and Zimmermann, 2000). Model structures can range from simple thermal envelopes or niches through to highly complex models that consider energy budgets across different life stages, food web interactions, and more. If habitat models can successfully define environmental constraints on species habitats using present-day data, those relationships can then be extrapolated into the future.

To date, most efforts using habitat modeling to predict climate change impacts on fish or fisheries have focused on adult life stages (Fogarty et al., 2008; Cheung et al., 2009; Astthorsson et al., 2012; Hare et al., 2012).

Application of larval or spawning habitat models to climate change research questions is less common, often due to a lack of species-level observations from egg and larval surveys. (Such observations are necessary in order to calibrate and/or validate models.) Additionally, environmental tolerances of adult and early life stages within species may be markedly different (Engelhard and Heino, 2006; Rijnsdorp et al., 2009; Lehodey et al., 2010; Muhling et al., 2011). As a result, models of climate impacts on adult fishes are unlikely to translate to larvae. To effectively model the consequences of climate change on early life history stages, two important questions must therefore be considered: how will climate change impact when and where fish reproduce, and how will it impact what larvae experience as they attempt to feed, grow, and survive?

The first question is generally more straightforward to address using habitat models. Where temperature limits on spawning and larval distribution are well described, and the underlying physiological and behavioral processes understood, relatively simple models can be used to predict changes in spawning behavior. For example, Muhling et al. (2011) used several decades of larval surveys and commercial fisheries catch data to define lower thermal limits of spawning initiation in Atlantic bluefin tuna

and upper limits of adult thermal tolerance. Habitat modeling results predicted a reduction in spring spawning habitat in the Gulf of Mexico throughout the remainder of the twenty-first century (Figure B1).

The second question is much more complex and has not been widely addressed. Potential changes in spawning activity have been estimated as part of broader models considering food web effects and adult distributions (e.g., Lehodey et al., 2010). Results from this research showed a general increase in predicted suitable spawning areas for bigeye tuna in the subtropical Pacific and some loss of spawning habitat in the tropics. However, to accurately predict the potential effects of climate change on larval survival and eventual recruitment, our understanding of how these processes operate under present conditions needs significant improvement. Temperature affects a multitude of physiological processes, yet drawing of robust connections between temperature and recruitment is generally rare (Myers, 1998; Sponaugle et al., 2006). In addition, recruitment is often determined at different points in early life stages of different species (Sissenwine, 1984; Leggett and Deblois, 1994). As a result, while the temporal and spatial extent of spawning can frequently be well predicted using simple temperature relationships, recruitment usually cannot.

It is important to note that an effective model of climate change impacts on larvae also needs to consider the dominant processes of greatest significance to the particular species of interest. The relative importance of an adequate food supply, sufficiently low predation pressure, and retention in a suitable environment will be distinct between an oceanic tuna, a coral reef fish, and a temperate gadoid or clupeiod species. The definition of "suitable" for each of these groups will also be completely different. While habitat models are an emerging tool for predicting climate change impacts on populations, they will only be as good as their input data. The more field and physiological data that are incorporated into model building, and the stronger the evidence for mechanistic links between species and their environments, the more confidence can be placed in model results. The implication is that, although habitat modeling techniques continue to move forward, the lack of basic ecological and physiological data may be a limiting factor in many situations. This limitation is especially true for the early life history stages of fishes, where these processes are poorly understood (Peck and Hufnagl, 2012; Peck et al., 2013).
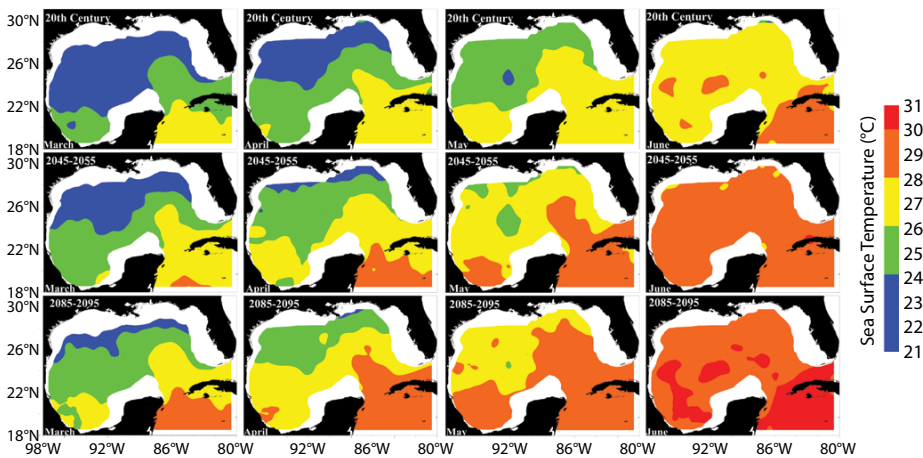

FIGURE B1. Predicted future change to spawning and larval habitat suitability for Atlantic bluefin tuna in the Gulf of Mexico based on outputs from predictive habitat models. Results are for the general months of spawning and larval presence (columns) in the twentieth century, mid-twenty-first century, and late twenty-first century (rows). *Modified from Muhling et al. (2011)*

Adults present – Below spawning limit

Highest adult catch rates – Favorable for spawning

Declining adult catch rates – Favorable for spawning

Physiologically stressful for adults – Upper limits of larval occcurence

Likely above adult physiological limits

CHANGES IN THE TEMPORAL AND SPATIAL DISTRIBUTIONS OF PRODUCTIVITY AND EARLY LIFE STAGES

Timing of life history processes is critical for many organisms to survive and grow. Marine fish, like many other organisms, have evolved to align the timing of their seasonal life cycle events (phenology) with environmental seasonality and other organisms' phenology in order to maximize survival. For many fish species, such relationships are particularly important during the vulnerable larval stage; this is, of course, fundamental to both Hjort's (1914, 1926) critical period hypothesis and Cushing's (1974, 1990) match-mismatch hypothesis. The temporal overlap of larvae with their preferred zooplankton prey is dependent upon the timing of both spawning and seasonal (e.g., spring) zooplankton blooms. Dynamics in the plankton are difficult to document, but even a small timing mismatch could theoretically have significant implications for recruitment variability due to the enormous numbers of fish larvae and the fact that slight changes in the proportion of larval survival can have major effects on recruitment to later stages (Houde, 1987).

In the context of climate change, phenology-related impacts are of critical importance because changes to either spawning or productivity blooms will yield an effect. Climate change will likely lead to mean directional shifts in the timing of spawning, as well as increased variability in the conditions (e.g., temperature) that influence phenology, potentially resulting in increasing frequency of mismatches. Although both fish larvae and their prey can and will exhibit shifts in phenology with changing conditions, synchrony of these shifts among trophic levels is unlikely (Hays et al., 2005). As yet, direct phenological effects of climate change on larval fish feeding success and later-stage recruitment have not been well documented. However, the likelihood for such effects is strongly supported by empirical evidence of changes

in the timing of plankton blooms as well as of fish spawning.

Usually, a mismatch occurs due to low covariability of biotic responses to changes in environmental cycles (e.g., light, temperature, and ocean stratification; Ji et al., 2010). For example, the spawning times of many fish populations in temperate and high latitudes are largely modulated by water temperature or photoperiod (Hutchings and Myers, 1994; Carscadden et al., 1997; Sims et al., 2004), and, though the data are limited, there is some evidence for climate change (temperature) effects on the temporal occurrence of fish larvae (Genner et al., 2010a; Asch, 2013). The timing of phytoplankton blooms, by contrast, is usually related to the degree of water column stratification, which can be affected by a variety of processes, including heat flux, wind stress, and freshwater input. In the seasonally ice-covered polar regions, the timing of ice advance and retreat could also play a critical role in controlling the timing of primary production processes (e.g., Kahru et al., 2011; Ji et al., 2013), which can further affect higher trophic levels, including zooplankton (Søreide et al., 2010) and fish populations (e.g., Hunt and Stabeno, 2002; Wassmann et al., 2011). Climate change has caused significant phenological shifts in many aquatic ecosystems (Sparks and Menzel, 2002; Durant et al., 2007; Poloczanska et al., 2013), and these shifts are likely to continue in the future, but the full implication of phenological mismatches for marine fish larvae and their prey under future climate scenarios requires further examination.

One difficulty is that the timing of a match or mismatch is not a simple matter. It has been suggested that abundance of either the consumer (Cushing, 1990) or its prey (Durant et al., 2005, 2007) can affect the degree of timing overlap, and high prey abundance could compensate for a small mismatch in the location or timing of the peaks. Therefore, simply using peak timing as the phenological index is probably not sufficient when

examining the match-mismatch between larval fish and their plankton prey. It is more important to know when and how long prey concentrations provide optimal feeding conditions. Thus, a comprehensive set of timing indices, such as start, peak, end, and duration of seasonal events is needed to systematically assess the phenology of target organisms (Ji et al., 2010).

Spatial variability of phenological patterns is another important consideration for larval fish survival. The optimal condition is a match between larvae and prey in both time and space (Figure 2A), while a mismatch in either (Figure 2B,C) or both (Figure 2D) is likely to negatively affect recruitment success. Cushing et al. (1990) discussed the spatial issue in an attempt to reconcile match-mismatch with the member/vagrant hypothesis proposed by Iles and Sinclair (1982). He pointed out that, within a larval retention area, a mismatch between the timing of spawning and prey production could be detrimental to fish larvae, and that larvae drifting away from the retention area would be subject to a spatial mismatch whether a temporal match is achieved or not. Thus, the degree of overlap between predator and prey is multifaceted.

It is not a trivial task to fully capture spatially explicit phenology patterns of plankton and larval fishes. Long-term plankton data sets with high temporal resolution are rare (Ji et al., 2010). Remote-sensing data can provide high-resolution estimates of phytoplankton, but they are limited to the surface layer of less turbid offshore waters and are only available for recent decades. Nevertheless, there are some successful examples of synthesizing remotely sensed ocean color data to explain the variability of larval fish survival (e.g., Platt and Csar Fuentes-Yaco, 2003), and the number of examples using this method is expected to increase as the time series become longer. Compared with phytoplankton, even fewer data are available for quantifying zooplankton phenology. A recent review by Mackas et al. (2012) compiled most of the available

time series, showing large (one to three months) interannual variability in the seasonal timing of some zooplankton taxa. Such variability is often correlated with anomalies of one (usually temperature) or more environmental variables. Data from long-term, large-scale surveys such as those using the Continuous Plankton Recorder (CPR) are extremely valuable because they allow detection of phenological shifts for both phytoplankton and zooplankton at the basin scale (Edwards and Richardson, 2004), and they also reveal clear cases where plankton community shifts are correlated with recruitment (e.g., Beaugrand et al., 2003).

A recent study (Siddon et al., 2013) assessed the consequence of spatial mismatches for walleye pollock and their zooplankton prey in the Bering Sea ecosystem, showing that warming has induced the separation of areas with high abundance of juvenile pollock and high zooplankton, and thus leading to low recruitment success. For fish larvae, which are far less mobile than juveniles, such a spatial mismatch, as determined by the distribution of spawning adults, would likely have greater effects. Climate-associated changes in the distribution of adults have been documented for a large number of fish species (Perry et al., 2005; Dulvy et al., 2008; Nye et al., 2009; Pinsky et al., 2013). For example, on the northeast continental shelf of the United States, 15 of 30 teleost species were found to have shifted north over a 40-year period (Nye et al., 2009). For some species, these spatial shifts will translate into a change in spawning distribution (and, thus, larval distribution), which has been evident in a number of species, including yellowtail flounder (Figure 3). However, other species tend to migrate to a fixed spawning location or region regardless of the prevailing conditions. Either scenario could result in a spatial mismatch between larvae and their preferred zooplankton prey, depending on the extent to which prey are also shifting. To date, analyses of spatial changes in both larval fish and their prey are rare, as are analyses across life

stages within a species. Yet, clearly, adding spatial dimensions to the phenological match-mismatch concept will be essential to a better understanding of climate impacts on larval fish dynamics.

CHANGES IN OVERALL PRODUCTIVITY

In addition to expected changes in the timing and location of productivity peaks, the absolute levels of primary and secondary production will also be affected by global change (Bopp et al., 2001; Behrenfeld et al., 2006). The specific nature of such effects will likely depend on latitudinal region as well as ecosystem type (Doney, 2006; Boyce et al., 2010; McQuatters-Gollop et al., 2011), though universal agreement on current and future patterns is still lacking. In temperate and subpolar latitudes, evidence suggests primary production will increase due to increased stratification (from warming and freshening) that will keep phytoplankton in the well-lit surface waters (Bopp et al., 2001; Doney, 2006). In upwelling ecosystems, winds favoring upwelling should increase (Bakun, 1990; Bakun et al., 2010; García-Reyes and Largier, 2010), but whether the greater intensity of upwelling will overcome the effects of increased water column stratification and result in greater productivity is somewhat uncertain (Auad et al.,
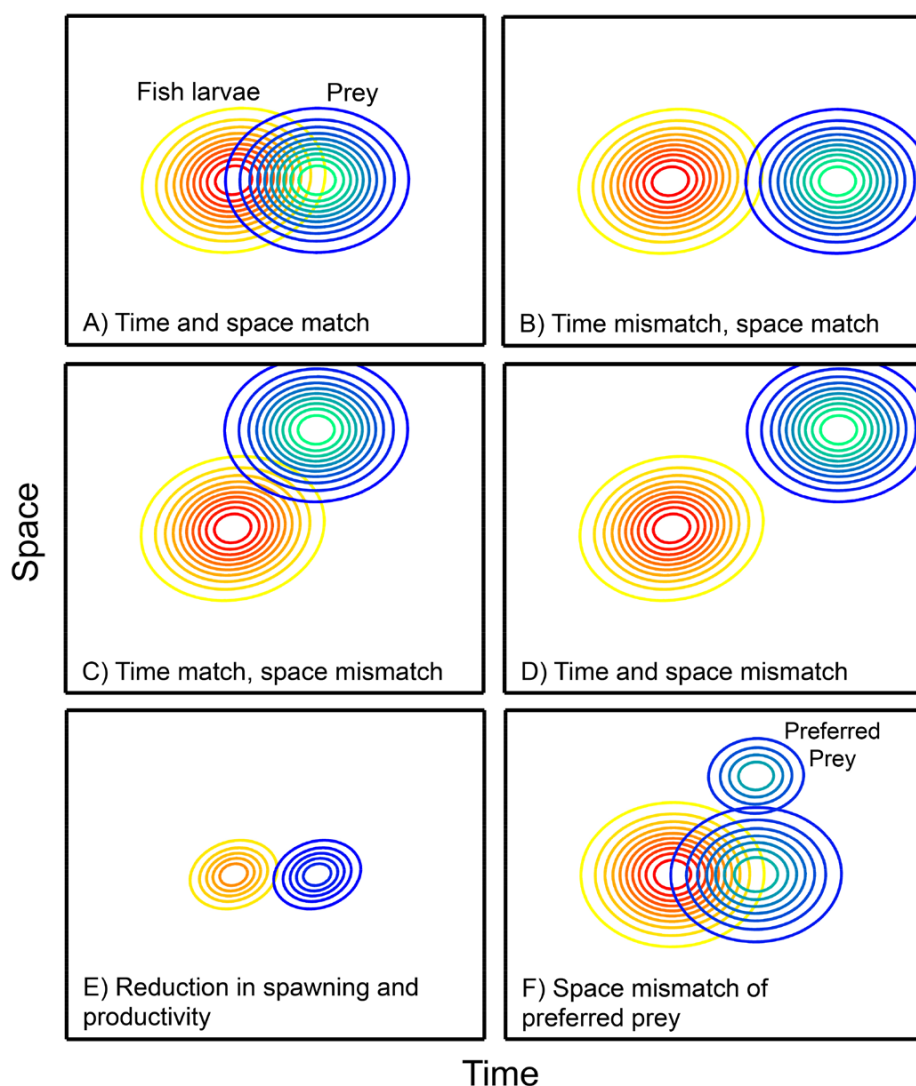

FIGURE 2. Conceptual diagram of matches and mismatches of fish larvae and their zooplankton prey in both time and space. Such spatial and temporal distributions are driven by the time and location of fish spawning, and the time and location of seasonal secondary productivity blooms. The abundance of both larvae and prey is higher at the center of the contours.

2006; King et al., 2011). In polar regions, increased temperatures are already reducing sea ice (and associated ice algae), not only resulting in major impacts on benthic ecosystems (Doney et al., 2012) but also leading to much greater phytoplankton production due to increased light availability (Arrigo et al., 2008). Even with these potential increases in production, the major disruptions to polar ecosystems from sea ice impacts could offset any benefits to fish populations conferred by greater zooplankton prey availability during the planktonic larval stage.

In lower latitudes, where the water column is already stratified, stratification is predicted to intensify, thereby reducing the degree of mixing of deep, nutrient-rich waters with sunlit surface waters and leading to a drop in net primary production (Behrenfeld et al., 2006). This could reduce zooplankton abundances and, thus, prey availability for the early life stages of fishes (Figure 2E). Less prey would add to the challenge already imposed by the temperature-induced increase in metabolic demands described above (McLeod et al., 2013). Interestingly, within the phytoplankton community, the proportional contribution and overall abundance of picophytoplankton is projected to increase with increasing temperatures (Morán et al., 2010), so that less-efficient transfer of nutrients up the food chain would result in food webs of low nutritional quality (Richardson, 2008). Such a shift could substantially alter the species composition of the

zooplankton community because some zooplankton taxa (e.g., pteropods and gelatinous organisms such as appendicularians) consume picophytoplankton quite well, while others (e.g., calanoid copepods) do not.

As zooplankton community composition changes, the effect on planktonic fish larvae will depend on each species' diet breadth and prey preferences. Mounting evidence suggests there is a broad spectrum in the degree of prey selectivity among larval fish taxa (Figure 4), with several taxa exhibiting highly selective feeding on particular prey types—including some larval fish taxa nearly exclusively consuming appendicularians or calanoid copepods (Llopiz and Cowen, 2009; Llopiz et al., 2010). Thus, shifts in zooplankton community and changes in abundance of preferred prey types (Figure 2F) mean that some larval fish taxa could be "winners," while others could be "losers" if they are unable to adapt to new prey regimes by changing what appear to be intrinsic, "hard-wired" preferences for particular prey types (Llopiz et al., 2010).

SYNERGISTIC EFFECTS OF FISHING AND CLIMATE CHANGE

Fishing impacts on early life history stages of marine fish operate through spawning adults. The number of offspring produced and the quality of those offspring can be severely impacted by both the quantity of mature adults removed from the population and the selective removal of some

components of the adult population. Removal of the largest, oldest fish in the population is an inherent consequence of fishing. Additionally, fishing pressure is typically applied unevenly across the spatial distribution of a population, again resulting in selective removal of discrete components of mature adults. Historically, management objectives have focused on the total biomass of mature females as the metric for the health of the population, with the characteristics of the females present in that spawning stock assumed to be inconsequential. However, severe declines in numerous species that were harvested at presumably sustainable levels have led many researchers to question the assumption that the composition of the spawning stock does not matter (Berkeley et al., 2004; Hsieh et al., 2006; Francis et al., 2007). If, as is typically assumed, year class strength is determined by the survival of early life stages, then the failure of the spawners to sustain the population presumably lies with the offspring they produce.

A growing body of literature is documenting the importance of maternal effects on multiple traits of early life stages of marine fishes (reviewed in Hixon et al., 2014). Among a diverse taxonomic range of species, older or larger females can have a substantial, disproportionate effect on the likelihood of larval survival, thereby engendering concern over the age/size truncation common to fisheries exploitation. Larger/older females can increase their reproductive success
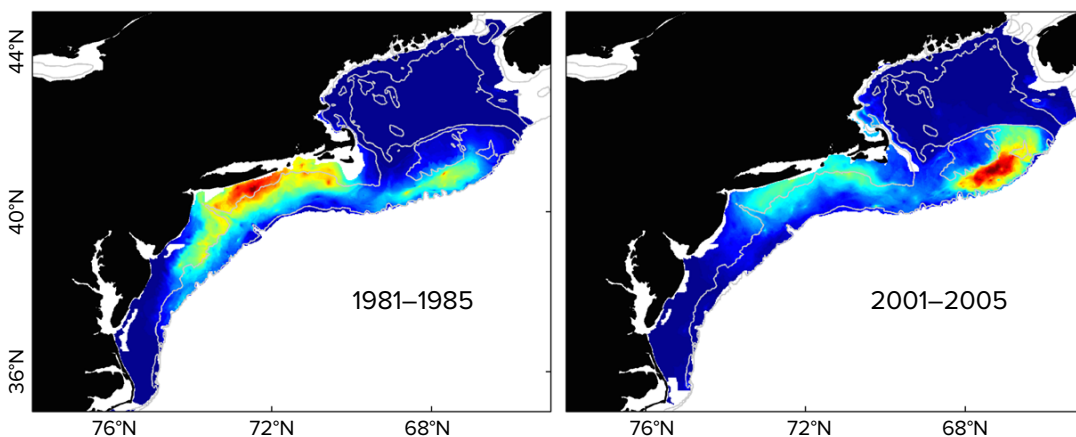

FIGURE 3. Changes in the spatial distribution of spawning yellowtail flounder from the early 1980s to the early 2000s (warmer colors represent higher densities). Such distributional shifts of spawning output lead to shifts in the distribution of larvae, which will likely influence the physical and prey environments experienced by the larvae, thereby affecting larval survival and recruitment.

relative to smaller/younger females via three primary mechanisms: (1) higher fecundity both on absolute (total eggs per batch, number of batches per season) and relative (eggs g⁻¹ female body weight) scales; (2) higher offspring quality (e.g., egg size, lipid content, larval performance); and (3) different spawning phenology (greater spread of reproduction across the season for batch spawners or different timing of spawning for total spawners; Figure 2E). The importance of such factors to population dynamics is a function of life history, with slow-growing, long-lived species thought to be more likely to rely on such reproductive strategies and more severely impacted by fishing-induced age or size truncation than fast-growing, short-lived species.

Habitat quality of the pelagic environment in which early life stages of most economically important marine fish species reside is highly variable in both space and time. Consequently, larval survival is thought to be dependent on a diversity of reproductive traits, constituting a bet hedging or portfolio strategy that increases the probability that at least some larvae are successful in each year. Diversity in spawning location and spawning timing may act to stabilize environmentally induced fluctuations in recruitment (Hixon et al., 2014). Indeed, a reduction in the age diversity of spawning adults has been associated with increased recruitment variability in a number of species (Marteinsdottir and Thorarinsson, 1998; Secor, 2000; Wieland et al., 2000; Hsieh et al., 2006).

The synergistic impacts of warming temperatures with intensive fishery exploitation will likely be a function of the diversity of reproductive behavior exhibited. When a population is subjected to substantial age truncation, the result is often younger, smaller fish that spawn later in the season (Hixon et al., 2014). This shift in spawning time could lead to more extreme mismatches of larval occurrence and prey availability, especially if ocean warming results in earlier peaks of primary production (as discussed above). Additionally, populations with high spatial variability in fishery concentration may lose the beneficial buffering effect of multiple spawning locations if warming temperatures impact the spawning activity of some regions more than others. Species that shift their distribution range in response to changing temperatures may retain their spawning phenology but will encounter a new spatial pattern of exploitation as fisheries adjust to their movement. In extreme cases, warmer temperatures may inhibit spawning altogether (Pankhurst and Munday, 2011), with clear losses to the spatial diversity of adults contributing to an annual cohort.

The interaction between exploitation patterns and physical changes in the ocean (e.g., increased stratification, altered currents, stronger upwelling) will again relate to the loss of age diversity by the disproportionate removal of older fish
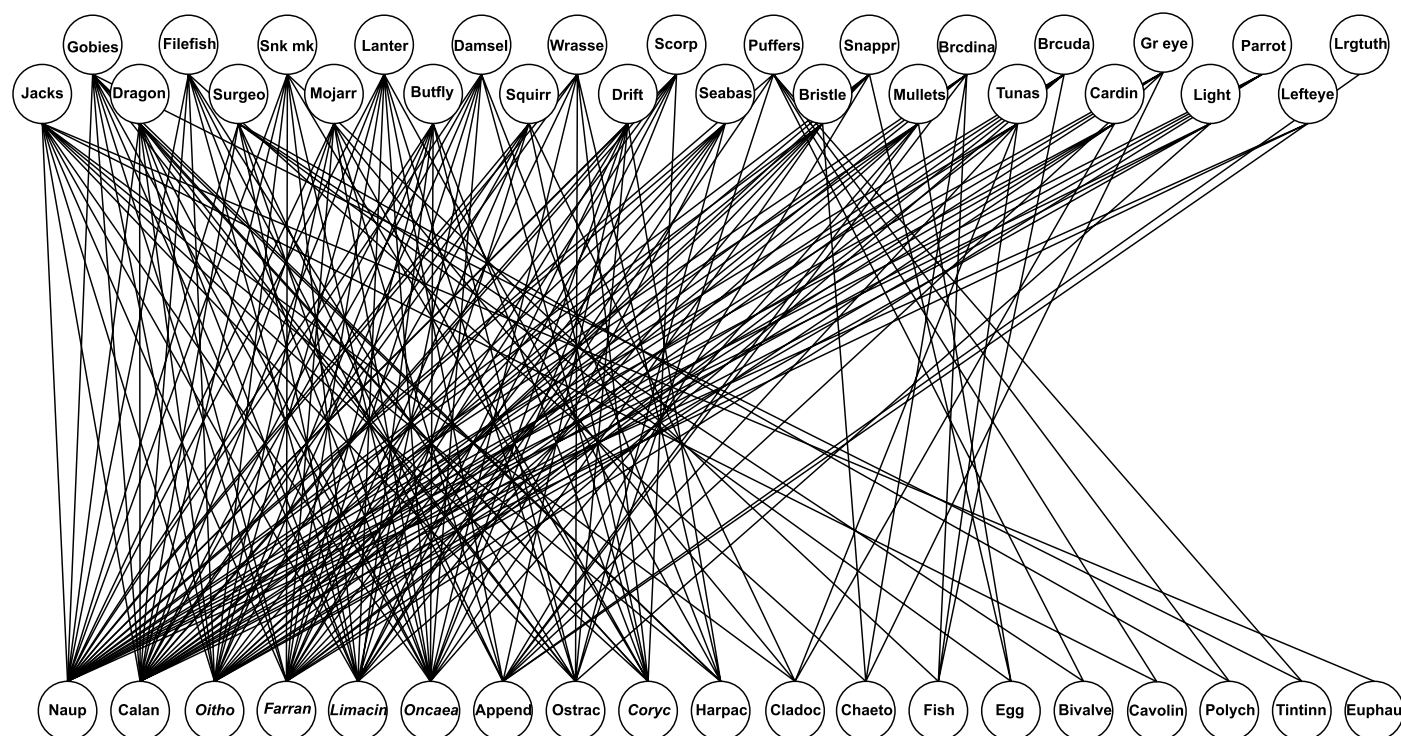

FIGURE 4. A food web for the tropical/subtropical oceanic waters in the Straits of Florida of 28 co-occurring larval fish families (which comprised 90% of all collected larvae; 4,704 larvae inspected) and their zooplankton prey. Links between fish families (upper rows) and prey (lower row) are present when a prey type contributed > 1% to the diet for the particular family. Larval fish families and prey are arranged left to right in decreasing order of the number of links. Families fall along a generalist-to-specialist gradient (evidenced by the number of links per family), indicating the potential for species-specific responses and sensitivities of fish larvae to any changes in zooplankton composition.

and spatial variability in fishery mortality rates. For example, many fish species in the California Current have long life spans, enabling them to persist through extended periods of poor environmental conditions (Longhurst, 2002). If climate change results in greater duration of oceanographic regimes unfavorable for larval survival, then the age truncation induced by fisheries will potentially exacerbate population declines by diminishing the bet hedging afforded by longevity. Likewise, spatial variation in the impacts of climate change on physical features, as noted by King et al. (2011) for a north-to-south gradient within the California Current, will interact with spatial variation in fishing pressure to affect the reproductive success of subpopulations contributing to a stock (Hsieh et al., 2008).

In general, we propose that intense fisheries exploitation will reduce the diversity of reproductive contributions for marine fishes encountering modified larval habitats as oceanographic factors respond to a changing climate. The significance of this interaction will likely vary markedly depending on life history strategy. Short-lived, rapidly growing, early maturing species may be more directly responsive to environmental shifts in their habitats, whereas long-lived, slow-growing, late-maturing species are more likely to exhibit the synergistic effects suggested here, as has been observed in long-term data sets of fish communities in the English Channel (Genner et al., 2010b).

LARVAL DISPERSAL AND POPULATION CONNECTIVITY IN A CHANGING OCEAN

Many of the changes outlined above, together with their direct and indirect effects on early life stages, will come together to impact the dispersal of eggs and larvae from spawning locations to settlement habitat (Munday et al., 2009c; Gerber et al., 2014). Most near-shore fishes disperse as pelagic larvae for a period of time prior to their metamorphosis into benthic habitat-associated juveniles and adults. The degree to which

the dispersal phase ecologically links geographically separated local populations (population connectivity) is often temporally and spatially variable, dependent on prevailing ocean currents as well as the biology and behavior of the larvae and adults (reviewed in Cowen and Sponaugle, 2009). Reproductive connectivity requires that successfully dispersing larvae then survive to successfully reproduce (Pineda et al., 2007). Successful larval dispersal under future projected climate change scenarios will depend on multiple variables, all of which are substantially influenced by changing ocean conditions (Figure 1).

In addition to the effects on productivity, increased vertical stratification of the water column will likely reduce the movement of organisms between layers and potentially change the direction and strength of horizontal currents. Large-scale ocean circulation such as the Atlantic meridional overturning circulation, driven by sinking of dense water at the poles, is expected to gradually slow over the next century (Bindoff et al., 2007; Meehl et al., 2007), with regional consequences (Liu et al., 2012). However, this and many other large-scale currents are also heavily influenced by environmental phenomena cycling on shorter time scales, such as the North Atlantic Oscillation, the Pacific Decadal Oscillation, and El Niño–Southern Oscillation (Bindoff et al., 2007). Interactions between climate change and the frequency and intensity of these decadal oscillations are as yet unknown. The strength of climatological effects on local circulation is expected to vary among locations. Changing water temperature, chemistry, and movement, in concert, will affect numerous processes associated with larval dispersal.

Potential reduction in suitable high-quality adult fish habitat due to ocean acidification, increased hypoxia, sea level rise, and other anthropogenic stressors such as pollution, coastal development, and overfishing, may lead to lower population abundances, affecting the cumulative number and location of

gametes spawned. For some species, temperature increases and subsequent geographical and temporal shifts in distribution ranges may result in higher adult population abundances and increased numbers of gametes (Hare et al., 2010), but for others the results may be negative (Donelson et al., 2010). Regardless of changes in population sizes, such shifts in the location and timing of the start of larval dispersal will interact with ocean circulation changes to result in new or modified dispersal pathways from adult to juvenile settlement habitats.

Once in the water column, larvae will be affected by changing current speeds and directions as well as the reduction in vertical shear in surface waters resulting from increased stratification. As a consequence, larval ontogenetic vertical migration may not have the same effect on transport trajectories as such behavior has today (Paris and Cowen, 2004; Huebert et al., 2011), potentially altering the extent of local retention vs. long-distance transport. Similarly, in regions where upwelling is enhanced, offshore transport of surface oriented larvae may be greater, thereby requiring more extensive coastal return mechanisms for late-stage larvae.

Superimposed on transport processes are factors that control the survival of larvae, many of which are outlined above. Where larvae manage to encounter patches of prey to sustain higher growth rates due to increased temperatures, their pelagic larval duration (PLD) is projected to be substantially lower due to the widespread linear relationship between growth rate and PLD (O'Connor et al., 2007). Theoretically, a shorter PLD may counter increased mortality rates with increasing temperature, but a shorter PLD simultaneously requires that larvae find suitable settlement habitat more rapidly. Another hurdle is that settlement habitats that benthic marine fishes seek at the end of their larval phases are increasingly fragmented due to a range of anthropogenic effects, and when compounded with compromised larval navigation ability in

high CO_2 waters (Munday et al., 2009a), as well as increased susceptibility to predation (Dixson et al., 2010; Munday et al., 2010; Ferrari et al., 2011), there is clear potential for major impacts on fish population sizes and compositions.

Recent efforts to estimate the effects of historical climate variability or project the effects of climate change on larval fish dispersal have focused on modeling the influence of temperature on PLD (O'Connor et al., 2007; Heath et al., 2008; Munday et al., 2009c; Huret et al., 2010). For some systems, effects of ocean acidification on larval growth, development, and navigation have also been included (Kendall et al., 2013), as well as temperature-related mortality rates or food availability (Tracey et al., 2012; Peck et al., 2013; Kristiansen et al., 2014). Changes in the vertical structure of the water column have been modeled in some studies to predict outcomes for larval survival and transport. For example, future recruitment to some small pelagic fisheries will be a function of the contrasting effects of predicted higher larval retention in stratified waters, a shoaling oxycline, and reduced nursery areas (Brochier et al., 2013). Due to the uncertainty in predicting ocean circulation changes, especially at local and even regional scales, few studies have incorporated changes in the speed or direction of currents (but see Vikebø et al., 2007; Munday et al., 2009c; Hidalgo et al., 2012). Hidalgo et al. (2012) show that changes in spawner distributions of cod and ocean circulation are the most important variables shaping future larval distributions, while temperature differences may influence distributions through changes in the spatial overlap of predators and prey.

By far the most precise models are those constructed from existing coupled individual-based and biophysical models that are parameterized with extensive empirical data (Miller, 2007; Werner et al., 2007). The most detailed examples of these have been developed for important fishery species such as cod (Vikebø et al., 2007; Hidalgo et al., 2012;

Kristiansen et al., 2014) and small pelagic fish (Peck et al., 2013), and physiological-based foraging and growth models have been applied to examine match-mismatch dynamics between larvae and their potential prey in a variety of other species (reviewed by Peck and Hufnagl, 2012). In some cases, highly useful models have been constructed for a diversity of marine species (Treml et al., 2012) or a generic marine species (Ayata et al., 2010; Lett et al., 2010; Huebert and Peck, 2014). Additional conceptual models lay a framework for interdisciplinary model development (King et al., 2011; Gerber et al., 2014). Aside from some of these modeling studies, documented or predicted changes in phytoplankton and zooplankton abundance and composition have rarely been factored into such models due to the lack of empirical data quantifying the role of these prey in larval fish diets. Yet, clearly, larval food availability underlies the degree to which thermally induced high larval metabolic rates can be translated into high larval growth and survival. Consequently, there is a need to collect additional empirical data on trophic interactions during the larval phase of many marine fishes (Llopiz, 2013). Larval feeding behavior (prey detection, swimming speeds) may also be affected by ocean acidification, and such experimental results should be included in models. In short, larval dispersal and population connectivity are likely to be quite reduced in the future ocean, but accurate prediction of these changes requires thorough parameterization of models with empirical data.

CONCLUSIONS AND FUTURE DIRECTIONS

It is a dynamic time to be conducting research on the early life stages of marine fishes. The tools at our fingertips have remarkable potential and, in recent decades, the nature of oceanographic research has become increasingly interdisciplinary. This bodes well for fully integrative studies of the variety of ways in which the early life stages of fishes interact

with and are affected by their environments. Although there is still much work to be done to improve our understanding of how early life processes relate to interannual and interdecadal recruitment variability, we are now charged with an additional task: elucidating how gradual, long-term changes to marine ecosystems will impact recruitment.

Many of the conclusions drawn here regarding anthropogenic impacts are necessarily speculative—there is relatively little concrete information about how the many direct, and especially indirect, mechanisms discussed will ultimately influence population replenishment. Future work should seek to strengthen our grasp on the impacts of individual stressors, but perhaps more importantly, it should pay special attention to the interacting effects of multiple stressors. Additionally, while documenting climate-related impacts on fish early life history is crucial, ultimately, we need to strive for developing a predictive capacity for understanding how future change will influence early life survival. This will enable effective and adaptive management strategies for fisheries and marine ecosystems as a whole. To this end, the value of long-term time series in examining global change impacts on marine ecosystems cannot be overstated. Continued and expanded funding for these efforts, as well as the establishment of new time series, will be necessary for observing and mitigating future impacts of global change on all life stages of ecologically and economically important fish species.

As noted by Houde (2008), we have long since emerged from Johan Hjort's shadow, and have expanded our investigations well beyond the first-feeding period of fish larvae and the role of starvation in recruitment variability. It is possible that, due to the interests and foci of major funding sources, as well as the "sexiness" of high-impact climate change findings, we may very well be under the new shadow of global-change-related early life history research—possibly at the expense of furthering our understanding

of fishery recruitment variability (Rice and Browman, 2014). In all likelihood, a balance of climate-related research on early life survival and more typical "recruitment fisheries oceanography" will be the most productive. Given the ubiquitous effects of global change on virtually all aspects of ecosystem function, the line between these two research trajectories will inevitably become blurred as we move further into the Anthropocene. ⬡

REFERENCES

Allan, B.J., P. Domenici, M.I. McCormick, S.-A. Watson, and P.L. Munday. 2013. Elevated CO_2 affects predator-prey interactions through altered performance. *PLoS One* 8(3)**:**e58520, http://dx.doi.org/10.1371/journal.pone.0058520.

Allan, B.J., G.M. Miller, M.I. McCormick, P. Domenici, and P.L. Munday. 2014. Parental effects improve escape performance of juvenile reef fish in a high-CO_2 world. *Proceedings of the Royal Society B*, http://dx.doi.org/10.1098/rspb.2013.2179.

Anderson, J.T. 1988. A review of size dependent survival during pre-recruit stages of fishes in relation to recruitment. *Journal of Northwest Atlantic Fishery Science* 8:55–66, http://journal.nafo.int/J08/anderson.pdf.

Arrigo, K.R., G. van Dijken, and S. Pabi. 2008. Impact of a shrinking Arctic ice cover on marine primary production. *Geophysical Research Letters* 35, L19603, http://dx.doi.org/10.1029/2008GL035028.

Asch, R.G. 2013. Interannual-to-decadal changes in phytoplankton phenology, fish spawning habitat, and larval fish phenology. PhD Dissertation, University of California, San Diego.

Astthorsson, O.S., H. Valdimarsson, A. Gudmundsdottir, and G.J. Óskarsson. 2012. Climate-related variations in the occurrence and distribution of mackerel (*Scomber scombrus*) in Icelandic waters. *ICES Journal of Marine Science* 69:1,289–1,297, http://dx.doi.org/10.1093/icesjms/fss084.

Auad, G., A. Miller, and E. Di Lorenzo. 2006. Long-term forecast of oceanic conditions off California and their biological implications. *Journal of Geophysical Research* 111, C09008, http://dx.doi.org/10.1029/2005JC003219.

Ayata, S.-D., P. Lazure, and É. Thiébaut. 2010. How does the connectivity between populations mediate range limits of marine invertebrates? A case study of larval dispersal between the Bay of Biscay and the English Channel (Northeast Atlantic). *Progress in Oceanography* 87:18–36, http://dx.doi.org/10.1016/j.pocean.2010.09.022.

Bailey, K.M., and E.D. Houde. 1989. Predation on eggs and larvae of marine fishes and the recruitment problem. *Advances in Marine Biology* 25:1–83.

Bakun, A. 1990. Global climate change and intensification of coastal ocean upwelling. *Science* 247:198–201, http://dx.doi.org/10.1126/science.247.4939.198.

Bakun, A., D.B. Field, A. Redondo-Rodriguez, and S.J. Weeks. 2010. Greenhouse gas, upwelling-favorable winds, and the future of coastal ocean upwelling ecosystems. *Global Change Biology* 16:1,213–1,228, http://dx.doi.org/10.1111/j.1365-2486.2009.02094.x.

Baumann, H., S.C. Talmage, and C.J. Gobler. 2012. Reduced early life growth and survival in a fish in direct response to increased carbon dioxide. *Nature Climate Change* 2:38–41, http://dx.doi.org/10.1038/nclimate1291.

Beaugrand, G., K.M. Brander, J.A. Lindley, S. Souissi, and P.C. Reid. 2003. Plankton effect on cod recruitment in the North Sea. *Nature* 426:661–664, http://dx.doi.org/10.1038/nature02164.

Behrenfeld, M.J., R.T. O'Malley, D.A. Siegel, C.R. McClain, J.L. Sarmiento, G.C. Feldman, A.J. Milligan, P.G. Falkowski, R.M. Letelier, and E.S. Boss. 2006. Climate-driven trends in contemporary ocean productivity. *Nature* 444:752–755, http://dx.doi.org/10.1038/nature05317.

Berkeley, S.A., M.A. Hixon, R.J. Larson, and M.S. Love. 2004. Fisheries sustainability via protection of age structure and spatial distribution of fish populations. *Fisheries* 29:23–32.

Bignami, S., I.C. Enochs, D.P. Manzello, S. Sponaugle, and R.K. Cowen. 2013a. Ocean acidification alters the otoliths of a pantropical fish species with implications for sensory function. *Proceedings of the National Academy of Sciences of the United States of America* 110:7,366–7,370, http://dx.doi.org/10.1073/pnas.1301365110.

Bignami, S., S. Sponaugle, and R.K. Cowen. 2013b. Response to ocean acidification in larvae of a large tropical marine fish, *Rachycentron canadum*. *Global Change Biology* 19:996–1,006, http://dx.doi.org/10.1111/gcb.12133.

Bindoff, N., J. Willebrand, V. Artale, A. Cazenave, J. Gregory, S. Gulev, K. Hanawa, C. Le Quere, S. Levitus, Y. Nojiri, and others. 2007. Observations: Oceanic climate change and sea level. Pp. 385–428 in *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Avery, M. Tignor, and H.L. Miller, eds, Cambridge University Press, Cambridge, UK, and New York, NY.

Bopp, L., P. Monfray, O. Aumont, J.L. Dufresne, H. Le Treut, G. Madec, L. Terray, and J.C. Orr. 2001. Potential impact of climate change on marine export production. *Global Biogeochemical Cycles* 15:81–99, http://dx.doi.org/10.1029/1999GB001256.

Boyce, D.G., M.R. Lewis, and B. Worm. 2010. Global phytoplankton decline over the past century. *Nature* 466:591–596, http://dx.doi.org/10.1038/nature09268.

Brauner, C., and D. Baker. 2009. Patterns of acid–base regulation during exposure to hypercarbia in fishes. Pp. 43–63 in *Cardio-Respiratory Control in Vertebrates*. M.L. Glass and S.C. Wood, eds, Springer.

Brochier, T., V. Echevin, J. Tam, A. Chaigneau, K. Goubanova, and A. Bertrand. 2013. Climate change scenarios experiments predict a future reduction in small pelagic fish recruitment in the Humboldt Current system. *Global Change Biology* 19:1,841–1,853, http://dx.doi.org/10.1111/gcb.12184.

Browman, H.I. 2014. Commemorating 100 years since Hjort's 1914 treatise on fluctuations in the great fisheries of northern Europe: Where we have

been, where we are, and where we are going. *ICES Journal of Marine Science* 71:1,989–1,992, http://dx.doi.org/10.1093/icesjms/fsu159.

Carscadden, J., B. Nakashima, and K. Frank. 1997. Effects of fish length and temperature on the timing of peak spawning in capelin (*Mallotus villosus*). *Canadian Journal of Fisheries and Aquatic Sciences* 54:781–787, http://dx.doi.org/10.1139/f96-331.

Chambers, R., A. Candelmo, E. Habeck, M. Poach, D. Wieczorek, K. Cooper, C. Greenfield, and B. Phelan. 2014. Effects of elevated CO_2 in the early life stages of summer flounder, *Paralichthys dentatus*, and potential consequences of ocean acidification. *Biogeosciences* 11:1,613–1,626, http://dx.doi.org/10.5194/bg-11-1613-2014.

Checkley, D.M., A.G. Dickson, M. Takahashi, J.A. Radich, N. Eisenkolb, and R. Asch. 2009. Elevated CO_2 enhances otolith growth in young fish. *Science* 324:1,683, http://dx.doi.org/10.1126/science.1169806.

Cheung, W.W., V.W. Lam, J.L. Sarmiento, K. Kearney, R. Watson, and D. Pauly. 2009. Projecting global marine biodiversity impacts under climate change scenarios. *Fish and Fisheries* 10:235–251, http://dx.doi.org/10.1111/j.1467-2979.2008.00315.x.

Chivers, D.P., M.I. McCormick, G.E. Nilsson, P.L. Munday, S.A. Watson, M.G. Meekan, M.D. Mitchell, K.C. Corkill, and M.C. Ferrari. 2014. Impaired learning of predators and lower prey survival under elevated CO_2: A consequence of neurotransmitter interference. *Global Change Biology* 20:515–522, http://dx.doi.org/10.1111/gcb.12291.

Chung, W.-S., N.J. Marshall, S.-A. Watson, P.L. Munday, and G.E. Nilsson. 2014. Ocean acidification slows retinal function in a damselfish through interference with GABAA receptors. *Journal of Experimental Biology* 217:323–326, http://dx.doi.org/10.1242/jeb.092478.

Collins, M., R. Knutti, J. Arblaster, J.-L. Dufresne, T. Fichefet, P. Friedlingstein, X. Gao, W.J. Gutowski, T. Johns, G. Krinner, and others. 2013. Long-term climate change: Projections, commitments and irreversibility. Chapter 12 in *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. T.F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, and P.M. Midgley, eds, Cambridge University Press, Cambridge, UK, and New York, NY.

Cowen, R.K., and S. Sponaugle. 2009. Larval dispersal and marine population connectivity. *Annual Review of Marine Science* 1:443–466, http://dx.doi.org/10.1146/annurev.marine.010908.163757.

Cushing, D.H. 1974. The natural regulation of fish populations. Pp. 399–412 in *Sea Fisheries Research*. F.R. Harden-Jones, ed., Elek Science, London.

Cushing, D.H. 1975. *Marine Ecology and Fisheries*. Cambridge University Press, 278 pp.

Cushing, D.H. 1990. Plankton production and year-class strength in fish populations: An update of the match/mismatch hypothesis. *Advances in Marine Biology* 26:249–293.

Devine, B., P. Munday, and G. Jones. 2012. Rising CO_2 concentrations affect settlement behaviour of larval damselfishes. *Coral Reefs* 31:229–238, http://dx.doi.org/10.1007/s00338-011-0837-0.

Dixson, D.L., P.L. Munday, and G.P. Jones. 2010. Ocean acidification disrupts the innate ability of fish to detect predator olfactory cues. *Ecology Letters* 13:68–75, http://dx.doi.org/10.1111/j.1461-0248.2009.01400.x.

Domenici, P., B. Allan, M.I. McCormick, and P.L. Munday. 2012. Elevated carbon dioxide affects behavioural lateralization in a coral reef fish. *Biology Letters* 8:78–81, http://dx.doi.org/10.1098/rsbl.2011.0591.

Donelson, J., P. Munday, M. McCormick, N.W. Pankhurst, and P. Pankhurst. 2010. Effects of elevated water temperature and food availability on the reproductive performance of a coral reef fish. *Marine Ecology Progress Series* 401:233–243, http://dx.doi.org/10.3354/meps08366.

Doney, S.C. 2006. Oceanography: Plankton in a warmer world. *Nature* 444:695–696, http://dx.doi.org/10.1038/444695a.

Doney, S.C., V.J. Fabry, R.A. Feely, and J.A. Kleypas. 2009. Ocean acidification: The other CO_2 problem. *Annual Review of Marine Science* 1:169–192, http://dx.doi.org/10.1146/annurev.marine.010908.163834.

Doney, S.C., M. Ruckelshaus, J.E. Duffy, J.P. Barry, F. Chan, C.A. English, H.M. Galindo, J.M. Grebmeier, A.B. Hollowed, and N. Knowlton. 2012. Climate change impacts on marine ecosystems. *Annual Review of Marine Science* 4:11–37, http://dx.doi.org/10.1146/annurev-marine-041911-111611.

Dulvy, N.K., S.I. Rogers, S. Jennings, V. Stelzenmüller, S.R. Dye, and H.R. Skjoldal. 2008. Climate change and deepening of the North Sea fish assemblage: A biotic indicator of warming seas. *Journal of Applied Ecology* 45:1,029–1,039, http://dx.doi.org/10.1111/j.1365-2664.2008.01488.x.

Durant, J.M., D.O. Hjermann, T. Anker-Nilssen, G. Beaugrand, A. Mysterud, N. Pettorelli, and N.C. Stenseth. 2005. Timing and abundance as key mechanisms affecting trophic interactions in variable environments. *Ecology Letters* 8:952–958, http://dx.doi.org/10.1111/j.1461-0248.2005.00798.x.

Durant, J.M., D.Ø. Hjermann, G. Ottersen, and N.C. Stenseth. 2007. Climate and the match or mismatch between predator requirements and resource availability. *Climate Research* 33:271–283, http://dx.doi.org/10.3354/cr033271.

Edwards, M., and A.J. Richardson. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* 430:881–884, http://dx.doi.org/10.1038/nature02808.

Engelhard, G.H., and M. Heino. 2006. Climate change and condition of herring (*Clupea harengus*) explain long-term trends in extent of skipped reproduction. *Oecologia* 149:593–603, http://dx.doi.org/10.1007/s00442-006-0483-3.

Esbaugh, A.J., R. Heuer, and M. Grosell. 2012. Impacts of ocean acidification on respiratory gas exchange and acid–base balance in a marine teleost, Opsanus beta. *Journal of Comparative Physiology B* 182:921–934.

Feely, R.A., S.C. Doney, and S.R. Cooley. 2009. Ocean acidification: Present conditions and future changes in a high-CO_2 world. *Oceanography* 22(4):36-47, http://dx.doi.org/10.5670/oceanog.2009.95.

Ferrari, M.C., R.P. Manassa, D.L. Dixson, P.L. Munday, M.I. McCormick, M.G. Meekan, A. Sih, and D.P. Chivers. 2012. Effects of ocean acidification on learning in coral reef fishes. *PLoS One* 7(2):e31478, http://dx.doi.org/10.1371/journal.pone.0031478.

Ferrari, M.C., M.I. McCormick, P.L. Munday, M.G. Meekan, D.L. Dixson, O. Lonnstedt, and D.P. Chivers. 2011. Putting prey and predator into the CO_2 equation: Qualitative and quantitative effects of ocean acidification on predator-prey interactions. *Ecology Letters* 14:1,143–1,148, http://dx.doi.org/10.1111/j.1461-0248.2011.01683.x.

Fogarty, M., L. Incze, K. Hayhoe, D. Mountain, and J. Manning. 2008. Potential climate change impacts on Atlantic cod (*Gadus morhua*) off the northeastern USA. *Mitigation and Adaptation Strategies for Global Change* 13:453–466, http://dx.doi.org/10.1007/s11027-007-9131-4.

Francis, R.C., M.A. Hixon, M.E. Clarke, S.A. Murawski, and S. Ralston. 2007. Ten commandments for ecosystem-based fisheries scientists. *Fisheries* 32:217–233, http://dx.doi.org/10.1577/1548-8446(2007)32[217:TCFBFS]2.0.CO;2.

Franke, A., and C. Clemmesen. 2011. Effect of ocean acidification on early life stages of Atlantic herring (*Clupea harengus* L.). *Biogeosciences Discussions* 8:7,097–7,126, http://dx.doi.org/10.5194/bg-8-3697-2011.

Frommel, A.Y., R. Maneja, D. Lowe, A.M. Malzahn, A.J. Geffen, A. Folkvord, U. Piatkowski, T.B. Reusch, and C. Clemmesen. 2012. Severe tissue damage in Atlantic cod larvae under increasing ocean acidification. *Nature Climate Change* 2:42–46, http://dx.doi.org/10.1038/nclimate1324.

Frommel, A.Y., A. Schubert, U. Piatkowski, and C. Clemmesen. 2013. Egg and early larval stages of Baltic cod, *Gadus morhua*, are robust to high levels of ocean acidification. *Marine Biology* 160:1,825–1,834, http://dx.doi.org/10.1007/s00227-011-1876-3.

Fuiman, L.A. 1986. Burst-swimming performance of larval zebra danios and the effects of diel temperature fluctuations. *Transactions of the American Fisheries Society* 115:143–148, http://dx.doi.org/10.1577/1548-8659(1986)115<143:BPOLZD>2.0.CO;2.

García-Reyes, M., and J. Largier. 2010. Observations of increased wind-driven coastal upwelling off central California. *Journal of Geophysical Research* 115, C04011, http://dx.doi.org/10.1029/2009JC005576.

Gemmell, B.J., J. Sheng, and E.J. Buskey. 2013. Compensatory escape mechanism at low Reynolds number. *Proceedings of the National Academy of Sciences of the United States of America* 110:4,661–4,666, http://dx.doi.org/10.1073/pnas.1212148110.

Genner, M.J., N.C. Halliday, S.D. Simpson, A.J. Southward, S.J. Hawkins, and D.W. Sims. 2010a. Temperature-driven phenological changes within a marine larval fish assemblage. *Journal of Plankton Research* 32:699–708, http://dx.doi.org/10.1093/plankt/fbp082.

Genner, M.J., D.W. Sims, A.J. Southward, G.C. Budd, P. Masterson, M. McHugh, P. Rendle, E.J. Southall, V.J. Wearmouth, and S.J. Hawkins. 2010b. Body size-dependent responses of a marine fish assemblage to climate change and fishing over a century-long scale. *Global Change Biology* 16:517–527, http://dx.doi.org/10.1111/j.1365-2486.2009.02027.x.

Gerber, L.R., M.D.M. Mancha-Cisneros, M.I. O'Connor, and E.R. Selig. 2014. Climate change impacts on connectivity in the ocean: Implications for conservation. *Ecosphere* 5(3):art33, http://dx.doi.org/10.1890/ES13-00336.1.

Guisan, A., and N.E. Zimmermann. 2000. Predictive habitat distribution models in ecology. *Ecological Modelling* 135:147–186, http://dx.doi.org/10.1016/S0304-3800(00)00354-9.

Hamilton, T.J., A. Holcombe, and M. Tresguerres. 2014. CO_2-induced ocean acidification increases anxiety in rockfish via alteration of GABAA receptor functioning. *Proceedings of the Royal Society B*, http://dx.doi.org/10.1098/rspb.2013.2509.

Hare, J.A. 2014. The future of fisheries oceanography lies in the pursuit of multiple hypotheses. *ICES Journal of Marine Science* 71:2,343–2,356, http://dx.doi.org/10.1093/icesjms/fsu018.

Hare, J.A., M.A. Alexander, M.J. Fogarty, E.H. Williams, and J.D. Scott. 2010. Forecasting the dynamics of a coastal fishery species using a coupled climate-population model. *Ecological Applications* 20:452–464, http://dx.doi.org/10.1890/08-1863.1.

Hare, J.A., M.J. Wuenschel, and M.E. Kimball. 2012. Projecting range limits with coupled thermal tolerance-climate change models: An example based on gray snapper (*Lutjanus griseus*) along the US East Coast. *PLoS One* 7(12):e52294, http://dx.doi.org/10.1371/journal.pone.0052294.

Hays, G.C., A.J. Richardson, and C. Robinson. 2005. Climate change and marine plankton. *Trends in Ecology & Evolution* 20:337–344, http://dx.doi.org/10.1016/j.tree.2005.03.004.

Heath, M.R., P.A. Kunzlik, A. Gallego, S.J. Holmes, and P.J. Wright. 2008. A model of meta-population dynamics for North Sea and West of Scotland cod: The dynamic consequences of natal fidelity. *Fisheries Research* 93:92–116, http://dx.doi.org/10.1016/j.fishres.2008.02.014.

Heuer, R.M., and M. Grosell. 2014. Physiological impacts of elevated carbon dioxide and ocean acidification on fish. *American Journal of Physiology - Regulatory, Integrative and Comparative Physiology* 307:R1,061–R1,084, http://dx.doi.org/10.1152/ajpregu.00064.2014.

Hidalgo, M., Y. Gusdal, G. Dingsør, D. Hjermann, G. Ottersen, L. Stige, A. Melsom, and N. Stenseth. 2012. A combination of hydrodynamical and statistical modelling reveals non-stationary climate effects on fish larvae distributions. *Proceedings of the Royal Society B* 279:275–283, http://dx.doi.org/10.1098/rspb.2011.0750.

Hixon, M.A., D.W. Johnson, and S.M. Sogard. 2014. BOFFFFs: On the importance of conserving old-growth age structure in fishery populations. *ICES Journal of Marine Science* 71:2,171–2,185, http://dx.doi.org/10.1093/icesjms/fst200.

Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. *Rapports et Proces-verbaux des Reunions, Conseil International pour l'Exploration de la Mer* 20:1–228.

Hjort, J. 1926. Fluctuations in the year classes of important food fishes. *Journal Du Conseil* 1(1):5–38.

Houde, E.D. 1987. Fish early life dynamics and recruitment variability. Pp. 17–29 in *American Fisheries Society Symposium Series*, vol. 2. R.D. Hoyt, ed., American Fisheries Society.

Houde, E.D. 1989. Comparative growth, mortality, and energetics of marine fish larvae: Temperature and implied latitudinal effects. *Fishery Bulletin* 87:471–495, http://fishbull.noaa.gov/873/houde.pdf.

Houde, E.D. 1997. Patterns and trends in larval-stage growth and mortality of teleost fish. *Journal of Fish Biology* 51:52–83, http://dx.doi.org/10.1111/j.1095-8649.1997.tb06093.x.

Houde, E.D. 2008. Emerging from Hjort's shadow. *Journal of the Northwest Atlantic Fishery Science* 41:53–70, http://dx.doi.org/10.2960/J.v41.m634.

Hsieh, C.H., H.J. Kim, W. Watson, E. Di Lorenzo, and G. Sugihara. 2009. Climate-driven changes in abundance and distribution of larvae of oceanic fishes in the southern California region. *Global Change Biology* 15:2,137–2,152, http://dx.doi.org/10.1111/j.1365-2486.2009.01875.x.

Hsieh, C.H., C.S. Reiss, R.P. Hewitt, and G. Sugihara. 2008. Spatial analysis shows that fishing enhances the climatic sensitivity of marine fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 65(5):947–961.

Hsieh, C.H., C.S. Reiss, J.R. Hunter, J.R. Beddington, R.M. May, and G. Sugihara. 2006. Fishing elevates variability in the abundance of exploited species. *Nature* 443:859–862, http://dx.doi.org/10.1038/nature05232.

Huebert, K.B., R.K. Cowen, and S. Sponaugle. 2011. Vertical migrations of reef fish larvae in the Straits of Florida and effects on larval transport. *Limnology and Oceanography* 56:1,653–1,666, http://dx.doi.org/10.4319/lo.2011.56.5.1653.

Huebert, K.B., and M.A. Peck. 2014. A day in the life of fish larvae: Modeling foraging and growth using Quirks. *PLoS One* 9(6):e98205, http://dx.doi.org/10.1371/journal.pone.0098205.

Hunt, G.L. Jr., and P.J. Stabeno. 2002. Climate change and the control of energy flow in the southeastern Bering Sea. *Progress in Oceanography* 55:5–22, http://dx.doi.org/10.1016/S0079-6611(02)00067-8.

Huret, M., P. Petitgas, and M. Woillez. 2010. Dispersal kernels and their drivers captured with a hydrodynamic model and spatial indices: A case

study on anchovy (*Engraulis encrasicolus*) early life stages in the Bay of Biscay. *Progress in Oceanography* 87:6–17, http://dx.doi.org/10.1016/j.pocean.2010.09.023.

Hurst, T.P., E.R. Fernandez, and J.T. Mathis. 2013. Effects of ocean acidification on hatch size and larval growth of walleye pollock (*Theragra chalcogramma*). *ICES Journal of Marine Science* 70:812–822, http://dx.doi.org/10.1093/icesjms/fst053.

Hurst, T.P., E.R. Fernandez, J.T. Mathis, J.A. Miller, C.M. Stinson, and E.F. Ahgeak. 2012. Resiliency of juvenile walleye pollock to projected levels of ocean acidification. *Aquatic Biology* 17:247–259, http://dx.doi.org/10.3354/ab00483.

Hutchings, J.A., and R.A. Myers. 1994. Timing of cod reproduction: Interannual variability and the influence of temperature. *Marine Ecology Progress Series* 108:21–32.

Hutchinson, G.E. 1957. Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology* 22:415–427.

Iles, T.D., and M. Sinclair. 1982. Atlantic herring: Stock discreteness and abundance. *Science* 215:627–633, http://dx.doi.org/10.1126/science.215.4533.627.

Ji, R., M. Edwards, D.L. Mackas, J.A. Runge, and A.C. Thomas. 2010. Marine plankton phenology and life history in a changing climate: Current research and future directions. *Journal of Plankton Research* 32:1,355–1,368, http://dx.doi.org/10.1093/plankt/fbq062.

Ji, R., M. Jin, and Ø. Varpe. 2013. Sea ice phenology and timing of primary production pulses in the Arctic Ocean. *Global Change Biology* 19:734–741, http://dx.doi.org/10.1111/gcb.12074.

Kahru, M., V. Brotas, M. Manzano-Sarabia, and B. Mitchell. 2011. Are phytoplankton blooms occurring earlier in the Arctic? *Global Change Biology* 17:1,733–1,739, http://dx.doi.org/10.1111/j.1365-2486.2010.02312.x.

Kendall, M.S., M. Poti, T.T. Wynne, B.P. Kinlan, and L.B. Bauer. 2013. Consequences of the life history traits of pelagic larvae on interisland connectivity during a changing climate. *Marine Ecology Progress Series* 489:43–59, http://dx.doi.org/10.3354/meps10432.

King, J.R., V.N. Agostini, C.J. Harvey, G.A. McFarlane, M.G. Foreman, J.E. Overland, E. Di Lorenzo, N.A. Bond, and K.Y. Aydin. 2011. Climate forcing and the California Current ecosystem. *ICES Journal of Marine Science* 68:1,199–1,216, http://dx.doi.org/10.1093/icesjms/fsr009.

Kirtman, B., S.B. Power, J.A. Adedoyin, G.J. Boer, R. Bojariu, I. Camilloni, F.J. Doblas-Reyes, A.M. Fiore, M. Kimoto, G.A. Meehl, and others. 2013. Near-term climate change: Projections and predictability. Chapter 11 in *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. T.F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, and P.M. Midgley, eds, Cambridge University Press, Cambridge, UK, and New York, NY.

Kristiansen, T., C. Stock, K.F. Drinkwater, and E.N. Curchitser. 2014. Mechanistic insights into the effects of climate change on larval cod. *Global Change Biology* 20:1,559–1,584, http://dx.doi.org/10.1111/gcb.12489.

Last, P.R., W.T. White, D.C. Gledhill, A.J. Hobday, R. Brown, G.J. Edgar, and G. Pecl. 2011. Long-term shifts in abundance and distribution of a temperate fish fauna: A response to climate change and fishing practices. *Global Ecology and Biogeography* 20:58–72, http://dx.doi.org/10.1111/j.1466-8238.2010.00575.x.

Leggett, W.C., and E. Deblois. 1994. Recruitment in marine fishes: Is it regulated by starvation and predation in the egg and larval stages? *Netherlands Journal of Sea Research* 32:119–134, http://dx.doi.org/10.1016/0077-7579(94)90036-1.

Lehodey, P., I. Senina, J. Sibert, L. Bopp, B. Calmettes, J. Hampton, and R. Murtugudde. 2010. Preliminary forecasts of Pacific bigeye tuna population trends under the A2 IPCC scenario. *Progress in Oceanography* 86:302–315, http://dx.doi.org/10.1016/j.pocean.2010.04.021.

Lett, C., S.-D. Ayata, M. Huret, and J.-O. Irisson. 2010. Biophysical modelling to investigate the effects of climate change on marine population dispersal and connectivity. *Progress in Oceanography* 87:106–113, http://dx.doi.org/10.1016/j.pocean.2010.09.005.

Liu, Y., S.K. Lee, B.A. Muhling, J.T. Lamkin, and D.B. Enfield. 2012. Significant reduction of the Loop Current in the 21st century and its impact on the Gulf of Mexico. *Journal of Geophysical Research* 117, C05039, http://dx.doi.org/10.1029/2011JC007555.

Llopiz, J.K. 2013. Latitudinal and taxonomic patterns in the feeding ecologies of fish larvae: A literature synthesis. *Journal of Marine Systems* 109–110:69–77, http://dx.doi.org/10.1016/j.jmarsys.2012.05.002.

Llopiz, J.K., and R.K. Cowen. 2009. Variability in the trophic role of coral reef fish larvae in the oceanic plankton. *Marine Ecology Progress Series* 381:259–272, http://dx.doi.org/10.3354/meps07957.

Llopiz, J.K., D.E. Richardson, A. Shiroza, S.L. Smith, and R.K. Cowen. 2010. Distinctions in the diets and distributions of larval tunas and the important role of appendicularians. *Limnology and Oceanography* 55:983–996, http://dx.doi.org/10.4319/lo.2010.55.3.0983.

Longhurst, A. 2002. Murphy's law revisited: Longevity as a factor in recruitment to fish populations. *Fisheries Research* 56:125–131, http://dx.doi.org/10.1016/S0165-7836(01)00351-4.

Mackas, D., W. Greve, M. Edwards, S. Chiba, K. Tadokoro, D. Eloire, M. Mazzocchi, S. Batten, A. Richardson, and C. Johnson. 2012. Changing zooplankton seasonality in a changing ocean: Comparing time series of zooplankton phenology. *Progress in Oceanography* 97:31–62, http://dx.doi.org/10.1016/j.pocean.2011.11.005.

Maneja, R., A. Frommel, A. Geffen, A. Folkvord, U. Piatkowski, M. Chang, and C. Clemmesen. 2013. Effects of ocean acidification on the calcification of otoliths of larval Atlantic cod *Gadus morhua*. *Marine Ecology Progress Series* 477:251–258, http://dx.doi.org/10.3354/meps10146.

Marteinsdottir, G., and K. Thorarinsson. 1998. Improving the stock-recruitment relationship in Icelandic cod (*Gadus morhua*) by including age diversity of spawners. *Canadian Journal of Fisheries and Aquatic Sciences* 55:1,372–1,377, http://dx.doi.org/10.1139/f98-035.

McCormick, M.I., S.-A. Watson, and P.L. Munday. 2013. Ocean acidification reverses competition for space as habitats degrade. *Scientific Reports* 3:3,280, http://dx.doi.org/10.1038/srep03280.

McLeod, I.M., J.L. Rummer, T.D. Clark, G.P. Jones, M.I. McCormick, A.S. Wenger, and P.L. Munday. 2013. Climate change and the performance of larval coral reef fishes: The interaction between temperature and food availability. *Conservation Physiology* 1(1):cot024, http://dx.doi.org/10.1093/conphys/cot024.

McQuatters-Gollop, A., P.C. Reid, M. Edwards, P.H. Burkill, C. Castellani, S. Batten, W. Gieskes, D. Beare, R.R. Bidigare, and E. Head. 2011. Is there a decline in marine phytoplankton? *Nature* 472:E6–E7, http://dx.doi.org/10.1038/nature09950.

Meehl, G.A., T.F. Stocker, W.D. Collins, P. Friedlingstein, A.T. Gaye, J.M. Gregory, A. Kitoh, R. Knutti, J.M. Murphy, A. Noda, and others 2007. Global climate projections. Pp. 747–845 in *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Avery, M. Tignor, and H.L. Miller, eds, Cambridge University Press, Cambridge, UK, and New York, NY.

Miller, G.M., S.-A. Watson, J.M. Donelson, M.I. McCormick, and P.L. Munday. 2012. Parental environment mediates impacts of increased carbon dioxide on a coral reef fish. *Nature Climate Change* 2:858–861, http://dx.doi.org/10.1038/nclimate1599.

Miller, T.J. 2007. Contribution of individual-based coupled physical-biological models to understanding recruitment in marine fish populations. *Marine Ecology Progress Series* 347:127–138, http://dx.doi.org/10.3354/meps06973.

Morán, X.A.G., Á. López-Urrutia, A. Calvo-Díaz, and W.K. Li. 2010. Increasing importance of small phytoplankton in a warmer ocean. *Global Change Biology* 16:1,137–1,144, http://dx.doi.org/10.1111/j.1365-2486.2009.01960.x.

Muhling, B.A., S.-K. Lee, J.T. Lamkin, and Y. Liu. 2011. Predicting the effects of climate change on bluefin tuna (*Thunnus thynnus*) spawning habitat in the Gulf of Mexico. *ICES Journal of Marine Science* 68:1,051–1,062, http://dx.doi.org/10.1093/icesjms/fsr008.

Munday, P.L., A.J. Cheal, D.L. Dixson, J.L. Rummer, and K.E. Fabricius. 2014. Behavioural impairment in reef fishes caused by ocean acidification at CO₂ seeps. *Nature Climate Change* 4:487–492, http://dx.doi.org/10.1038/nclimate2195.

Munday, P.L., D.L. Dixson, J.M. Donelson, G.P. Jones, M.S. Pratchett, G.V. Devitsina, and K.B. Døving. 2009a. Ocean acidification impairs olfactory discrimination and homing ability of a marine fish. *Proceedings of the National Academy of Sciences of the United States of America* 106:1,848–1,852, http://dx.doi.org/10.1073/pnas.0809996106.

Munday, P.L., D.L. Dixson, M.I. McCormick, M. Meekan, M.C. Ferrari, and D.P. Chivers. 2010. Replenishment of fish populations is threatened by ocean acidification. *Proceedings of the National Academy of Sciences of the United States of America* 107:12,930–12,934, http://dx.doi.org/10.1073/pnas.1004519107.

Munday, P.L., J.M. Donelson, D.L. Dixson, and G.G. Endo. 2009b. Effects of ocean acidification on the early life history of a tropical marine fish. *Proceedings of the Royal Society B* 276:3,275–3,283, http://dx.doi.org/10.1098/rspb.2009.0784.

Munday, P.L., V. Hernaman, D.L. Dixson, and S.R. Thorrold. 2011. Effect of ocean acidification on otolith development in larvae of a tropical marine fish. *Biogeosciences* 8:1,631–1,641, http://dx.doi.org/10.5194/bg-8-1631-2011.

Munday, P., J. Leis, J. Lough, C. Paris, M. Kingsford, M. Berumen, and J. Lambrechts. 2009c. Climate change and coral reef connectivity. *Coral Reefs* 28:379–395, http://dx.doi.org/10.1007/s00338-008-0461-9.

Munday, P.L., M.S. Pratchett, D.L. Dixson, J.M. Donelson, G.G. Endo, A.D. Reynolds, and R. Knuckey. 2013. Elevated CO₂ affects the behavior of an ecologically and economically important coral reef fish. *Marine Biology* 160:2,137–2,144, http://dx.doi.org/10.1007/s00227-012-2111-6.

Murray, C.S., A. Malvezzi, C.J. Gobler, and H. Baumann. 2014. Offspring sensitivity to ocean acidification changes seasonally in a coastal marine fish. *Marine Ecology Progress Series* 504:1–11, http://dx.doi.org/10.3354/meps10791.

Myers, R.A. 1998. When do environment–recruitment correlations work? *Reviews in Fish Biology and Fisheries* 8:285–305, http://dx.doi.org/10.1023/A:1008828730759.

Nilsson, G.E., D.L. Dixson, P. Domenici, M.I. McCormick, C. Sørensen, S.-A. Watson, and P.L. Munday. 2012. Near-future carbon dioxide levels alter fish behaviour by interfering with neurotransmitter function. *Nature Climate Change* 2:201–204, http://dx.doi.org/10.1038/nclimate1352.

Nye, J.A., J.S. Link, J.A. Hare, and W.J. Overholtz. 2009. Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. *Marine Ecology Progress Series* 393:111–129, http://dx.doi.org/10.3354/meps08220.

O'Connor, M.I., J.F. Bruno, S.D. Gaines, B.S. Halpern, S.E. Lester, B.P. Kinlan, and J.M. Weiss. 2007. Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. *Proceedings of the National Academy of Sciences of the United States of America* 104:1,266–1,271, http://dx.doi.org/10.1073/pnas.0603422104.

Pankhurst, N.W., and P.L. Munday. 2011. Effects of climate change on fish reproduction and early life history stages. *Marine and Freshwater Research* 62:1,015–1,026, http://dx.doi.org/10.1071/MF10269.

Paris, C.B., and R.K. Cowen. 2004. Direct evidence of a biophysical retention mechanism for coral reef fish larvae. *Limnology and Oceanography* 49:1,964–1,979, http://dx.doi.org/10.4319/lo.2004.49.6.1964.

Peck, M.A., K.B. Huebert, and J.K. Llopiz. 2012. Intrinsic and extrinsic factors driving match-mismatch dynamics during the early life history of marine fishes. *Advances in Ecological Research* 47:177–302, http://dx.doi.org/10.1016/B978-0-12-398315-2.00003-X.

Peck, M.A., and M. Hufnagl. 2012. Can IBMs tell us why most larvae die in the sea? Model sensitivities and scenarios reveal research needs. *Journal of Marine Systems* 93:77–93, http://dx.doi.org/10.1016/j.jmarsys.2011.08.005.

Peck, M.A., P. Reglero, M. Takahashi, and I.A. Catalán. 2013. Life cycle ecophysiology of small pelagic fish and climate-driven changes in populations. *Progress in Oceanography* 116:220–245, http://dx.doi.org/10.1016/j.pocean.2013.05.012.

Pepin, P. 1991. Effect of temperature and size on development, mortality, and survival rates of the pelagic early life-history stages of marine fish. *Canadian Journal of Fisheries and Aquatic Sciences* 48:503–518, http://dx.doi.org/10.1139/f91-065.

Perry, A.L., P.J. Low, J.R. Ellis, and J.D. Reynolds. 2005. Climate change and distribution shifts in marine fishes. *Science* 308:1,912–1,915, http://dx.doi.org/10.1126/science.1111322.

Pimentel, M., M. Pegado, T. Repolho, and R. Rosa. 2014. Impact of ocean acidification in the metabolism and swimming behavior of the dolphinfish (*Coryphaena hippurus*) early larvae. *Marine Biology* 161:725–729, http://dx.doi.org/10.1007/s00227-013-2365-7.

Pineda, J., J.A. Hare, and S. Sponaugle. 2007. Larval transport and dispersal in the coastal ocean and consequences for population connectivity. *Oceanography* 20(3):22–39, http://dx.doi.org/10.5670/oceanog.2007.27.

Pinsky, M.L., B. Worm, M.J. Fogarty, J.L. Sarmiento, and S.A. Levin. 2013. Marine taxa track local climate velocities. *Science* 341:1,239–1,242, http://dx.doi.org/10.1126/science.1239352.

Platt, T., and K.T.F. Csar Fuentes-Yaco. 2003. Marine ecology: Spring algal bloom and larval fish survival. *Nature* 423:398–399, http://dx.doi.org/10.1038/423398b.

Poloczanska, E.S., C.J. Brown, W.J. Sydeman, W. Kiessling, D.S. Schoeman, P.J. Moore, K. Brander, J.F. Bruno, L.B. Buckley, and M.T. Burrows. 2013. Global imprint of climate change on marine life. *Nature Climate Change* 3:919–925, http://dx.doi.org/10.1038/nclimate1958.

Pope, E., R. Ellis, M. Scolamacchia, J. Scolding, A. Keay, P. Chingombe, R. Shields, R. Wilcox, D. Speirs, and R. Wilson. 2014. European sea bass, *Dicentrarchus labrax*, in a changing ocean. *Biogeosciences* 11:2,519–2,530, http://dx.doi.org/10.5194/bg-11-2519-2014.

Pörtner, H.-O., and M. Peck. 2010. Climate change effects on fishes and fisheries: Towards a cause-and-effect understanding. *Journal of Fish Biology* 77:1,745–1,779, http://dx.doi.org/10.1111/j.1095-8649.2010.02783.x.

Rice, J., and H.I. Browman. 2014. Where has all the recruitment research gone, long time passing? *ICES Journal of Marine Science* 71:2,293–2,299, http://dx.doi.org/10.1093/icesjms/fsu158.

Richardson, A.J. 2008. In hot water: Zooplankton and climate change. *ICES Journal of Marine Science* 65:279–295, http://dx.doi.org/10.1093/icesjms/fsn028.

Rijnsdorp, A.D., M.A. Peck, G.H. Engelhard, C. Möllmann, and J.K. Pinnegar. 2009. Resolving the effect of climate change on fish populations. *ICES Journal of Marine Science* 66:1,570–1,583, http://dx.doi.org/10.1093/icesjms/fsp056.

Rummer, J.L., C.S. Couturier, J.A. Stecyk, N.M. Gardiner, J.P. Kinch, G.E. Nilsson, and P.L. Munday. 2014. Life on the edge: Thermal optima for aerobic scope of equatorial reef fishes are close to current day temperatures. *Global Change Biology* 20:1,055–1,066, http://dx.doi.org/10.1111/gcb.12455.

Sabine, C.L., R.A. Feely, N. Gruber, R.M. Key, K. Lee, J.L. Bullister, R. Wanninkhof, C. Wong, D.W. Wallace, and B. Tilbrook. 2004. The oceanic sink for anthropogenic CO_2. *Science* 305:367–371, http://dx.doi.org/10.1126/science.1097403.

Secor, D. 2000. Longevity and resilience of Chesapeake Bay striped bass. *ICES Journal of Marine Science* 57:808–815, http://dx.doi.org/10.1006/jmsc.2000.0560.

Shoji, J., S.-i. Toshito, K.-i. Mizuno, Y. Kamimura, M. Hori, and K. Hirakawa. 2011. Possible effects of global warming on fish recruitment: Shifts in spawning season and latitudinal distribution can alter growth of fish early life stages through changes in daylength. *ICES Journal of Marine Science* 68:1,165–1,169, http://dx.doi.org/10.1093/icesjms/fsr059.

Siddon, E.C., T. Kristiansen, F.J. Mueter, K.K. Holsman, R.A. Heintz, and E.V. Farley. 2013. Spatial match-mismatch between juvenile fish and prey provides a mechanism for recruitment variability across contrasting climate conditions in the eastern Bering Sea. *PLoS One* 8(12):e84526, http://dx.doi.org/10.1371/journal.pone.0084526.

Simpson, S.D., P.L. Munday, M.L. Wittenrich, R. Manassa, D.L. Dixson, M. Gagliano, and H.Y. Yan. 2011. Ocean acidification erodes crucial auditory behaviour in a marine fish. *Biology Letters* 7:917–920, http://dx.doi.org/10.1098/rsbl.2011.0293.

Sims, D.W., V.J. Wearmouth, M.J. Genner, A.J. Southward, and S.J. Hawkins. 2004. Low-temperature-driven early spawning migration of a temperate marine fish. *Journal of Animal Ecology* 73:333–341, http://dx.doi.org/10.1111/j.0021-8790.2004.00810.x.

Sinclair, M. 1997. Prologue. Recruitment in fish populations: The paradigm shift generated by ICES Committee A. Pp. 1–27 in *Early Life History and Recruitment in Fish Populations*. Springer.

Sissenwine, M.P. 1984. Why do fish populations vary? Pp. 59–94 in *Exploitation of Marine Communities, Dahlem Workshop Report,* vol. 32. Springer, http://dx.doi.org/10.1007/978-3-642-70157-3_3.

Søreide, J.E., E. Leu, J. Berge, M. Graeve, and S. Falk-Petersen. 2010. Timing of blooms, algal food quality and *Calanus glacialis* reproduction and growth in a changing Arctic. *Global Change Biology* 16:3,154–3,163, http://dx.doi.org/10.1111/j.1365-2486.2010.02175.x.

Sparks, T.H., and A. Menzel. 2002. Observed changes in seasons: An overview. *International Journal of Climatology* 22:1,715–1,725, http://dx.doi.org/10.1002/joc.821.

Sponaugle, S., K. Grorud-Colvert, and D. Pinkard. 2006. Temperature-mediated variation in early life history traits and recruitment success of the coral reef fish *Thalassoma bifasciatum* in the Florida Keys. *Marine Ecology Progress Series* 308:1–15, http://www.int-res.com/abstracts/meps/v308/feature.

Sunday, J.M., P. Calosi, S. Dupont, P.L. Munday, J.H. Stillman, and T.B. Reusch. 2014. Evolution in an acidifying ocean. *Trends in Ecology & Evolution* 29:117–125, http://dx.doi.org/10.1016/j.tree.2013.11.001.

Tewksbury, J.J., R.B. Huey, and C.A. Deutsch. 2008. Putting the heat on tropical animals. *Science* 320:1,296, http://dx.doi.org/10.1126/science.1159328.

Tracey, S.R., K. Hartmann, and A.J. Hobday. 2012. The effect of dispersal and temperature on the early life history of a temperate marine fish. *Fisheries Oceanography* 21:336–347, http://dx.doi.org/10.1111/j.1365-2419.2012.00628.x.

Treml, E.A., J.J. Roberts, Y. Chao, P.N. Halpin, H.P. Possingham, and C. Riginos. 2012. Reproductive output and duration of the pelagic larval stage determine seascape-wide connectivity of marine populations. *Integrative and Comparative Biology* 52:525–537, http://dx.doi.org/10.1093/icb/ics101.

Vikebø, F., S. Sundby, B. Ådlandsvik, and O. Otterå. 2007. Impacts of a reduced thermohaline circulation on transport and growth of larvae and pelagic juveniles of Arcto-Norwegian cod (*Gadus morhua*). *Fisheries Oceanography* 16(3):216–228, http://dx.doi.org/10.1111/j.1365-2419.2007.00427.x.

von Herbing, I.H. 2002. Effects of temperature on larval fish swimming performance: The importance of physics to physiology. *Journal of Fish Biology* 61:865–876, http://dx.doi.org/10.1111/j.1095-8649.2002.tb01848.x.

Wang, M., J.E. Overland, and N.A. Bond. 2010. Climate projections for selected large marine ecosystems. *Journal of Marine Systems* 79:258–266, http://dx.doi.org/10.1016/j.jmarsys.2008.11.028.

Wassmann, P., C.M. Duarte, S. Agusti, and M.K. Sejr. 2011. Footprints of climate change in the Arctic marine ecosystem. *Global Change Biology* 17:1,235–1,249, http://dx.doi.org/10.1111/j.1365-2486.2010.02311.x.

Welch, M.J., S.-A. Watson, J.Q. Welsh, M.I. McCormick, and P.L. Munday. 2014. Effects of elevated CO_2 on fish behaviour undiminished by transgenerational acclimation. *Nature Climate Change* 4:1,086–1,089, http://dx.doi.org/10.1038/nclimate2400.

Werner, F.E., R.K. Cowen, and C.B. Paris. 2007. Coupled biological and physical models: Present capabilities and necessary developments for future studies of population connectivity. *Oceanography* 20(3):54–69, http://dx.doi.org/10.5670/oceanog.2007.29.

Wieland, K., A. Jarre-Teichmann, and K. Horbowa. 2000. Changes in the timing of spawning of Baltic cod: Possible causes and implications for recruitment. *ICES Journal of Marine Science* 57:452–464, http://dx.doi.org/10.1006/jmsc.1999.0522.